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# A MONOGRAPH OF THE RECENT CEPHALOPODA

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# A MONOGRAPH OF THE RECENT CEPHALOPODA

BASED ON THE COLLECTIONS IN THE
BRITISH MUSEUM (NATURAL HISTORY)

## PART II

## THE OCTOPODA

(EXCLUDING THE OCTOPODINAE)

*By*

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# PREFACE

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W. T. Calman,
*Keeper of Zoology.*

*British Museum (Natural History),*
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NATURAL
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# A MONOGRAPH OF THE RECENT CEPHALOPODA

## PART II.

### I. INTRODUCTION.

#### (*a*) General

This volume contains a systematic review of all the groups included in the order Octopoda, with the exception of the large subfamily Octopodinae, which was dealt with in the first part of this Monograph. It also contains an account of the morphology of the Octopoda as a whole, including the extinct suborder Palaeoctopoda. The survey of the Octopodinae in the first volume was mainly devoted to systematic details, the morphology of the suborder Incirrata, in which the Octopodinae are placed, being but slightly sketched. The order is now examined comprehensively and the relationship of the various subordinate groups and their evolutionary history are discussed.

The Octopoda are one of the two main divisions of the Dibranchiate Cephalopods. The other order, the Decapoda, which includes the squids and cuttlefishes, is a group which has received a good deal of attention. Their habits and distribution render them easy of capture, and the abundance of their fossil remains has made them an object of study for over a century. The Octopoda, on the other hand, have received far less notice. The Octopodinae, in which the Common Octopus of European waters is placed, have been frequently studied and observed. The Paper Nautilus (*Argonauta*) has been an object of popular and scientific interest for a long time. It was used as an artistic *motif* in Minoan Crete and provided T. H. Huxley with the material for one of his celebrated zoological epigrams. Nevertheless, the bulk of the genera placed in this order are but little known even to the zoologist, and their morphology and classification have attracted the attention of only a few specialists. This is largely due to the fact that the majority are abyssal or mid-water forms which remained unknown till modern deep-sea investigation was developed. Moreover, owing to their habits, they are usually obtained as single specimens and the process of accumulating good series and information concerning them has been slow and laborious.

These animals are exclusively marine in habitat. They have a world-wide distribution and a very considerable vertical range. One would characterize the group as "subabyssal," at least in the adult stage, and it is worth noting that representatives of the genera that are more regularly found in shallow water and at the surface, have also been taken in deep hauls.

The Octopoda are essentially carnivorous animals. Some of the abyssal forms may be carrion- or débris-eaters, and it has been suggested

that some live on plankton. The littoral Octopodinae are active and capable of vigorous movement. They are wary creatures with highly developed parental instincts and display manipulatory skill and considerable intelligence and individuality. The Argonautida are gregarious and the females are probably predatory. One of them at least (*Ocythoë*), to judge by its musculature, must be vigorous and active. The rest of the order, as far as we may judge from their structure, are more inert. The deep-water forms tend to be highly modified. They have gelatinous bodies and externally are often medusiform and bizarre in appearance.

Some Octopoda attain a very considerable size. The Giant Octopus of the N.E. Pacific, alluded to in Vol. I, is probably the largest member of the group. *Alloposus* and a few of the Cirromorpha seem to attain considerable dimensions and *Ocythoë tuberculata* may reach a total length of over three feet.

The systematic study of this group of animals and the preparation of a scheme of classification force us to consider several problems of general interest. (1) Many of the species live, as we have said, in deep water and exhibit striking modifications which seem to be related to this mode of life. The interpretation of these modifications is essential to an understanding of the classification and evolution of the group as a whole. (2) The order offers us a very attractive field of morphological speculation, in so far as its relationship to the Decapoda is concerned. If the view adopted here is correct, the various suborders of Octopoda have each an array of special characters which resemble those of the Decapoda, and the tracing of the relationships of these groups to the other great Dibranchiate order is of considerable interest.

The classification and morphology of this group are, however, by no means easy problems. Only a single extinct genus is known at present, and it is difficult to decide if the resemblances between various groups are due to relationship or to convergence. The same difficulty is met in discussing the order as a whole. Thus we find a marked and peculiar resemblance between the Sepiolidae (Decapoda) and the Octopoda in the suspensory architecture of the visceral sac, a resemblance which can hardly be due to relationship. If these remotely related groups have acquired such a remarkable resemblance by convergence, we shall be prepared to consider that certain resemblances between various groups of Octopoda may be of this nature. A full discussion of this fundamental problem would be out of place in this work, as it would necessitate a very detailed discussion on all the organ-systems of the group. Actually the time is not ripe for such an exhaustive survey. The anatomy of many critical forms is unknown (especially among the Vampyromorpha), and several of the organ-systems require a careful comparative study as to structure and function. The embryology of all but a few genera is unknown and, as we have seen, only one extinct genus has so far been described. In this volume I have attempted, first, to give a comprehensive account of the morphology of the group as a whole; secondly, to indicate the chief evolutionary tendencies and to relate them, as far as is possible, to the habits and lives of the animals themselves, and, thirdly, to construct as reasonable a system of classification as possible. I have not attempted to discuss the problem of Octopod relationship, *i.e.* whether they are descended from one or another of the great Decapod groups, from

a more generalized Decapod stock, or even directly from the Tetrabranchiata. This problem can only be considered after a review of Decapod morphology. I have, however, been at some pains to point out the special resemblances between the Octopoda and Decapoda and to discuss their significance.

On the whole, the Octopoda and Decapoda resemble each other in numerous features which tend to be of a simple and generalized character (*e.g.* some of the Octopoda resemble the Decapoda in having a gill-structure of a simple type). But in some of the resemblances specialized structures are involved, *e.g.* funnel-valve, complex adhesive apparatus, statocysts of a certain type. If I am right in supposing that these structures are homologous in the two groups, the Octopoda must have diverged from the Decapod stem at a fairly advanced stage in the evolution of the latter. This would be, of course, somewhat surprising. I admit that our means of judging the morphological value of the various characters are very unsatisfactory (p. 36). But it is clear that we have before us two very interesting alternatives. Either, as suggested above, the Octopoda came off the common Dibranchiate stock at a relatively advanced stage in its evolution and after it had acquired certain special structures, or else there has been a very considerable amount of convergence between the two orders in respect of highly specialized organs. I believe the former view is correct and that the older idea of a radical difference between the two orders is erroneous. It remains, however, to be seen if this opinion is borne out by the results of Decapod morphology.

As the discussion on the phylogeny and evolution of the group is long and contains a good deal of detail, I have supplied a general summary on this subject (p. 62).

### (*b*) Historical.

The history of the study of the Octopodinae has already been sketched (Vol. I, p. 5). Of the forms discussed here only *Eledone* and the Argonautida were known to the early students such as Blainville, Orbigny, Delle Chiaje and Lamarck. The deep-water forms were practically unknown. Eschricht's *Cirroteuthis mülleri* was described in 1838, and the genus was mentioned by Orbigny (1845) in his later work and by Gray (1849). Progress was slow and nearly half a century elapsed before any large additions to our knowledge were made. In 1873 Verrill published the first of a long series of papers in which several Cirromorph and Eledonellid forms, as well as sundry deep-water Octopodids, were described from North-east American waters. A further instalment of knowledge was provided by Hoyle in his " Challenger " report (1886). The continued development of the technique of deep-sea investigation brought further information on all the groups concerned from Joubin, Hoyle and Chun. The latter and his pupils (W. T. Meyer and A. Ebersbach), Ijima and Ikeda, Berry, Grimpe and the present writer increased our knowledge of the Cirromorpha. Chun himself (1915) made a valuable contribution in his study of the Ctenoglossa. Joubin (1912, 1920 and 1929) and Thiele (1915) laid the foundation of our study of the Vampyromorpha, the first species of which was figured by Chun (1903). In 1929 I pointed out the archaic characters of the Vampyromorpha and, following the suggestion of Grimpe, explored

the characters of the deep-water Octopodids (1924*a*, 1926*a*, 1927). In the meantime Naef and Grimpe had done important work in reorganizing the classification, and Naef had increased our knowledge of the Argonautida and of the embryology of the group (1923, 1928). In general there may be said to be urgent need of more embryological study, and there are many aspects of Cirromorph and Vampyromorph morphology which require elucidation. The bionomics of the deep-sea forms are as yet imperfectly known and we are very much in the dark as to the feeding-habits and reproduction of these creatures. The subject of their adaptation was reviewed by Abel (1916) and myself (1926*a*), but our knowledge is very far from satisfactory. Finally it may be noted that but a single extinct genus (*Palaeoctopus*) and some extinct Argonautid species are known. Steinmann's novel views (1925) as to the relation between the Argonautida and Ammonites must be mentioned.

The wider question of the relationship of the Octopoda to the Decapoda was dealt with in a masterly essay by Brock (1880); but, owing to subsequent discoveries, his views now require modification.

## II. THE MORPHOLOGY OF THE ORDER OCTOPODA.

The general plan and orientation of the Octopod body have been described in Part I (p. 6). That description is applicable to all the members of the order, but some amplification of the original account is desirable. As originally stated, the visceral sac is not in contact with the mantle over all its surface, but is suspended from it at certain points, the method of suspension differing from that found in the body of most Decapoda and affording perhaps the most fundamental difference between the two orders. The points at which suspension is established are seven (Brock, 1880, p. 210), viz. the neck-region, the apex of the body, the

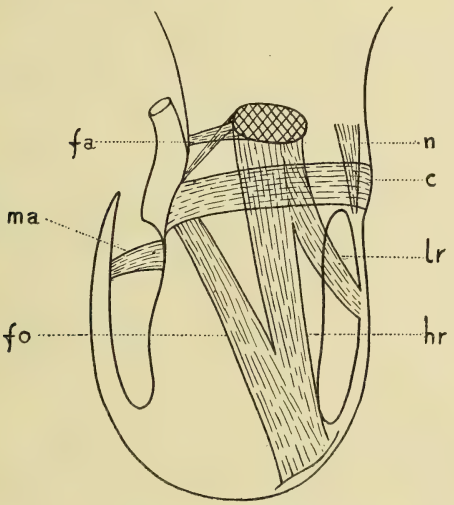



Fig. 1.—Diagram of the musculature of a typical Octopod. (After W. T. Meyer.)

*c*, collaris; *lr*, lateral mantle retractor; *hr*, head retractor; *fo*, funnel depressor; *ma*, median adductor; *n*, nuchalis; *fa*, funnel-adductor.

median ventral line (where the median pallial adductor is inserted into the visceral sac for a short distance behind the anus) and two areas on each side of the body, where the funnel depressors and the lateral pallial adductors are inserted into the viscero-cephalic mass. It is open to question whether the funnel depressor should, as Brock thinks, rank as a separate suspensory element, as its insertion (Fig. 1) is more or less involved in the apical union. Some useful speculation might be devoted to the profound difference between the architecture of the Decapod and Octopod bodies and its relation to differences of locomotion. Furthermore, it is necessary to note the resemblance in this respect between the Sepiolidae (Decapoda) and the Octopoda. Brock (*l.c.*, p. 219), who rightly points out that, if the muscular system alone were concerned, the

Sepiolidae might be regarded as the " dekapode Stammform " of the Octopoda, believes that the resemblance is due to convergence. The Sepiolidae are mainly benthic and fossorial, and at first sight this appears to give us a clue to the origin of the convergence, as many Octopoda are benthic. We know very little, however, about the suspensory mechanism in the most archaic Octopods (Vampyromorpha), and obviously the condition of a nektonic form like *Ocythoë*, which resembles the benthic forms in this respect, is an argument against an intimate relationship between mode of life and the form of the suspensory architecture. It should be noted that in some of the Argonautida (Brock, *l.c.*, p. 207) the neck-union, though present, is very imperfectly developed and seems to approach the Decapod condition. In some Vampyromorpha and *Cirroteuthis* the median adductor is absent (a Decapod feature). In certain Cirromorpha the dorsal cavity between the nuchal and apical junctions is partly obliterated (? secondarily). In three distinct forms *Retroteuthis*, *Alloposus hardyi* and *Heptapus* there is a very peculiar modification of the general architecture of the body, in that the web and arms (velar area) have rotated backwards through as much as 90% and become largely adherent to the tissue of the dorsal-mantle region. Arising as outgrowths from the mantle in the dorsal-lateral region of the Vampyromorpha, Cirromorpha and Paleoctopoda, are found one or two pairs of fins, the homology of which with those of the Decapoda is discussed on p. 37. The alleged occurrence of a finned form of Octopodine (*Pinnoctopus*) is discussed in Part I (p. 7).

In many forms which are devoid of fins cutaneous ridges are sometimes found encircling the periphery of the body. These are particularly noticeable in *Bathypolypus arcticus* and certain " Eledonid " forms. Naef (1923, p. 675, footnote) thinks that, because the fins in *Grimpoteuthis mawsoni* are continued up the sides of the body towards the eyes, the peripheral ridges may be " reaktivierte Flossenrudimente." I would point out, however, that in many Octopodids the peripheral ridges are found in the ventro-lateral region and, therefore, are not very likely to be homologous with fins.

The arms are eight in number and were, no doubt, primitively equal in length, but they are usually differentiated in this respect. This differentiation and the " arm-formula " employed to express it is described in Part I (p. 9). The oral surface of the arms is flattened and bears one or two rows of suckers. These are circular and cup-like and are nearly always sessile. In certain Vampyromorpha and in *Palaeoctopus* some or all of the suckers are pedunculate as in the Decapoda. In the Argonautida they are elongated (though not pedunculate) and connected by a continuous membrane like the " Schutzsäume " of the Decapoda, the nature of which is discussed on p. 38.

In the Vampyromorpha and Cirromorpha the arms bear on the outer edges outside the suckers a double series of filiform processes (cirri) which alternate with the suckers. The function of these is unknown, though it has variously been suggested that they are sensory or used for forming food-currents (see p. 120). In most of the Incirrata one arm is modified in the male as an intromittent organ (hectocotylus) (p. 15). The identification of the arms with those of the Decapoda, in which the eight sessile arms are accompanied by two tentacles, has been much discussed. Naef (1923, p. 655) believes that the third arm of the Octopoda is homologous

with the Decapod tentacle (see p. 94). In the Vampyromorpha alone there is a pair of " filaments " projecting from pouches in the web between the first and second arms. These arise from the circumoral muscular mass and are innervated from the pedal ganglion and have therefore been treated as vestiges of one of the pairs of Decapod appendages. The identity of the filaments and of the Octopod arms is discussed on p. 93.

In most of the Octopoda the web is well-developed between the arms and is bilaterally symmetrical, forming characteristic shapes for which I have proposed a method of description by means of a " web formula " (Vol. I, p. 7). In the Cirromorpha the web tends to become extremely deep and to extend nearly to the extremity of the arms. The use of the web in locomotion and the possibility that it supersedes the funnel as a locomotor organ are considered on pp. 56–58.

The head is usually well-defined, except in the Cirromorpha. In *Vitreledonella* it is very small. In some abyssal forms the eyes are of enormous size. In one genus (*Amphitretus*) they are " telescopic " and in *Cirrothauma* they are atrophied.

In the Vampyromorpha light-organs are found on various parts of the outer surface, and it is assumed that the peculiarly modified suckers (p. 165) of *Cirrothauma* are of this nature. In addition to the species in which definite light-organs are recorded, there are two other forms noted as " phosphorescent " or " luminous," though there is no definite information as to the source of light. These are " *Octopus gracilis*," Eydoux and Souleyet (1852, p. 14), and *Eledonella* sp. (Gardiner and Cooper, 1907, p. 25). Darwin (1870, p. 8) noted that sundry " Octopods " were luminous. This may have been due, as Berry (1920*a*, p. 147) suggests, to infection by luminous bacteria. A " small Octopod " is also recorded by Giglioli (MS. in Berry, *l.c.*, p. 172) as having a whitish light. In the *Eledonella* there are evidently definite organs, as Gardiner and Cooper describe it as " set with minute black specks each giving a tiny spark of rather blue phosphorescent light."

The only other noteworthy external features are the pouches on the oral surface of the web in *Cistopus* (Vol. I, p. 182) and the so-called " water pores " in *Ocythoë* and *Tremoctopus*, which lead into the " head cavities ". Naef (*l.c.*, p. 802) has pointed out that cavities of this kind are characteristic of nektonic Dibranchiata. Their precise function is unknown.

The skin of various forms bears during early development a coating of bristles of various kinds. These have been noted in the Octopodinae, *Eledone*, *Scaeurgus*, *Tremoctopus*, *Argonauta* and *Ocythoë*. These or similar bristles sometimes persist into adult life (individuals of *Bathypolypus arcticus*). In *Ocythoë* the skin is closely beset with hard-pointed tubercles which have the consistency of cartilage, but are formed of " festen Cutisgewebe " (Naef, *l.c.*, p. 755).

The funnel is situated, as in the other Dibranchiata, on the ventral side. When free, it lies in a slight depression in the ventral side of the head. Among a good many abyssal and pelagic forms it is largely involved in the tissues of the head, and as a consequence must lose the power of directing its jet both backwards and forwards (see p. 119). It is a simple tubular structure provided with a glandular funnel-organ of varying shape. In the Vampyromorpha alone there is an internal valve, which is situated, like that of the Decapoda, just below the siphonal orifice.

The mantle-aperture was probably widely open in the primitive Cephalopoda, and it is in this condition in the Vampyromorpha and most of the Incirrata. In many Cirromorpha it is very narrow as the result of a progressive lateral fusion of the mantle-edge with the tissues of the head and is barely large enough to allow the funnel to project through it. In *Chunioteuthis* this reduction is so marked that the mantle-aperture coincides with that of the funnel. By a different process (median as well as lateral fusion) it is reduced in *Amphitretus* to two lateral pores. A similar process is seen in some Decapoda.

The funnel is, of course, an important organ of locomotion, its actual motive power being derived from the forcible expulsion of the water contained in the pallial cavity through its narrow aperture. In the Decapoda in which there is no median adductor, this expulsion must be brought about by the circular muscles of the mantle. It is important that

Fig. 2.—Diagram of adhesive-organ in the Cephalopoda.

(The cephalic component is dotted, the pallial component being white.)
(*a*) Decapod; (*b*) *Argonauta*; (*c*) *Ocythoë*; (*d*) *Tremoctopus*; (*e*) *Octopus*.
(From specimens in Brit. Mus.)

in *Cirroteuthis* there is no median adductor and in other Cirromorpha it tends to be very small. Whether its absence in *Cirroteuthis* implies a lessened or modified use of the funnel I cannot say. It is curious that *Opisthoteuthis*, which is assumed to be a benthic and probably a burrowing form, has a more normal adductor (Meyer, *l.c.*, p. 194). The functional significance of the closure of the mantle-cavity is discussed on pp. 28 and 57. The funnel is temporarily locked to the edge of the mantle by the so-called adhesive organ. This consists of two cartilaginous pieces on each side, one of which (the cephalic element) is on the funnel, the other (the pallial element) on the inner edge of the mantle immediately opposite the cephalic element. The two elements fit into each other in various ways. In the Octopodidae the cephalic element is a prominent ridge that fits into a shallow groove in the mantle. In the Vampyromorpha there is an arrangement like that of the Decapoda, the cephalic element being hollow (" negative ") and receiving a prominent boss, the (" positive ") pallial element. The Argonautida show an interesting series of gradations from this to the Octopodid form. There is no adhesive system in the Cirromorpha and Ctenoglossa. It is a striking fact that in the Octopodidae the system is very weak, as contrasted with the highly

efficient system seen in some Decapods and *Ocythoë* among the Argonautida. The modification of the adhesive organ, the closure of the pallial cavity, the variation in size and muscularity of the funnel and the presence or absence of the adductor pallii medianus certainly suggest a wide range of variation in locomotor activity. Probably we should include the web and fins (pp. 20 and 22) in the system of locomotor organs. I have thought it desirable to tabulate below these modifications of the pallial, etc., organs in the various groups.

| | *Decapoda.* (normal) | *Vampyromorpha.* | *Cteno-glossa.* | *Cirro-teuthis.* | *Argonautida.* | *Octopus.* |
|---|---|---|---|---|---|---|
| *Body musculature.* | Strong. | Moderate –feeble. | Feeble. | Feeble. | Strong–moderate | Strong. |
| *Funnel.* | „ | Large (? strong). | Moderate. | Moderate. | Large. | Large. |
| *Pallial aperture.* | Wide. | Wide. | Wide. | Narrow. | Wide. | Wide. |
| *Pallial adductor.* | Absent. | (?). | Present. | Absent. | Present. | Present. |
| *Adhesive organ.* | Strong. | Usually present. | Absent. | Absent. | Strong. –moderate. | Weak. |
| *Web.* | Absent. | Deep. | Moderate –deep. | Deep. | Absent. | Moderate. |
| *Fins.* | Present. | Present. | Absent. | Present. | Absent. | Absent. |

I have omitted from this list specialized types such as *Chunioteuthis*, the abyssal Heteroglossa, etc.

*Alimentary System.* The mouth is surrounded by a pair of lips. These are of simple form (? except in *Hansenoteuthis* and *Ocythoë*) and there is no marked development outside the lips of a " Buccaltrichter " as in the Decapoda. The jaws are always present and well developed except in one or two instances (e.g. *Amphitretus thielei*, Robson (1930*b*, p. 384)). The radula either consists of nearly similar (homodont) teeth (Vampyromorpha, *Argonauta*) or else the teeth are differentiated into rhachidian, first, second and third laterals and marginal plates of characteristic shape (Heteroglossa, *Tremoctopus*). The Cirromorpha are devoid of a radula and the dentition of sundry abyssal Heteroglossa shows marked degeneration.

The morphology of the Cephalopod radula is a difficult question, but the main points at issue must be stated here, as the various resemblances and differences among the Octopoda are too striking to be ignored.

The chief feature in this group is that we find in the radula of both Decapoda and Octopoda two distinct tendencies. In the Sepioidea among the Decapods and the Vampyromorpha and *Argonauta* among the Octopoda the teeth are unicuspid and more or less homodont, and the only marked modification in the first three teeth is that the base of the second lateral becomes rather elongate. In the Teuthoidea (e.g. *Loligo*, *Ommatostrephes*) (Text-fig. 5) among the Decapoda and in *Ocythoë* and the Heteroglossa among the Octopoda the teeth are provided with additional cusps and tend to become markedly differentiated.

The critical question, as far as the Octopoda are concerned, is—which is the primitive form, the unicuspid homodont or the multicuspid heterodont? Is the Vampyromorph radula primarily or secondarily simple, or, conversely, is that of *Ocythoë* primarily or secondarily heterodont and multicuspid?

A good deal depends on this question, for if it is found that the homodont radula is primitive in the Octopoda it is probable that it is also primitive in the Decapoda and the case for regarding the Sepioidea and not the Teuthoidea as the most primitive Decapoda, is strengthened (but

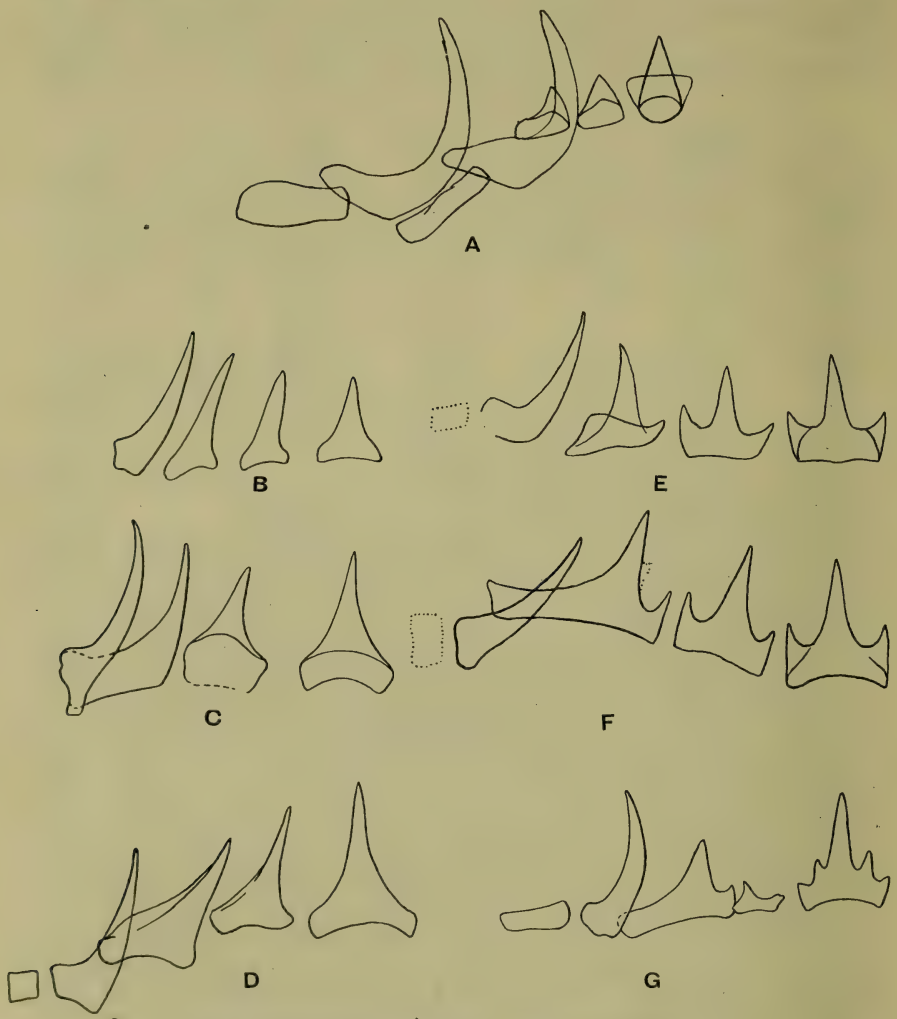



Fig. 3.—The Cephalopod Radula (diagrammatic).

A, *Nautilus pompilius* (B.M.); B, *Sepia officinalis* (B.M.); C, *Melanoteuthis beebei* (P.Z.S.); D, *Argonauta argo* (B.M.); E, *Loligo* sp. (P.Z.S.); F, *Ocythoë tuberculata* (B.M.); G, *Octopus vulgaris* (B.M.).

not necessarily proved). As far as the radula is concerned I put forward the view that the Vampyromorph-Sepioid type is primitive (1929*a*, p. 479). Brock (1880, p. 237) thinks the Sepioid type is the most evolved among the Decapoda, and Naef (1921, p. 122) cites the radula of *Sepia* and that of *Loligo* (with extra cusps) as typical of his ideal "Protodibranchus."

To decide this question we can consider the evolution of the radula

itself and also the general morphological status of the animal possessing it. Following the latter argument we might assert (*e.g.*) that, as the Teuthoidea or *Ocythoë* are found to be more primitive, their radula probably represents the primitive type. This is by no means an infallible inference.

The argument from the radula alone helps us little. We do not know which of the types described here is more primitive within the class. We may think that a row of unicuspid, similar teeth is likely to be more archaic on general grounds, but this is not necessarily true. My friend Col. Peile informs me that many embryonic Gastropod radulae are multicuspid and become simple in the adult stage. The more archaic Gastropods and Amphineura have teeth that vary a good deal. Those of the Amphineura are mainly unicuspid, but, much differentiated in size. The

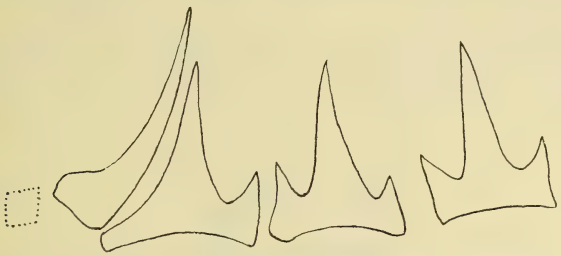


Fig. 4.—*Ocythoë tuberculata.* Radula (based on the figures of Brock and Jatter).

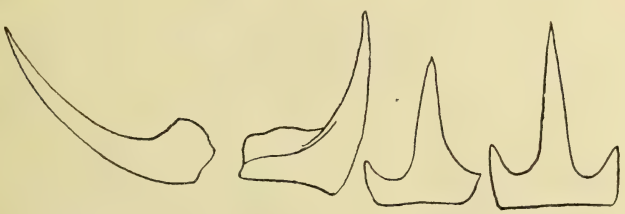


Fig. 5.—*Ommatostrephes illecebrosa.* Radula (see p. 9).

Docoglossate Gastropods may have bicuspid and tricuspid laterals and the teeth in the Rhipidoglossa are differentiated. The truth is that we cannot even guess what the primitive Molluscan radula was like. Among the Cephalopoda some argument for the original simplicity of the Dibranchiate type may be derived from the unicuspid teeth of *Nautilus* (Fig. 3a); but the radula of *Nautilus* is already specialized in its enormous curved laterals.

The argument from the status of the group itself is not very helpful. Perhaps the most significant fact is that the Vampyromorpha, in which the radula is simple, are without much doubt more primitive than the other Octopoda. On the other hand, I agree with Naef (1923, p. 730) that *Argonauta* (which has a unicuspid radula) is more evolved than any of its associates, so that here we find the more evolved type with a simple radula. What I think requires very careful examination is the nature of the resemblance between the radula of *Ocythoë* and that of the Teuthoidea. Naef (*l.c.*, p. 755) says that the former " erinnert auffallend an die der

Teuthoidea." Actually (*id.*, 1921, pl. 16, f. 8) he shows a radula which is remarkably like that of the Teuthoidea. But (cf. Fig. 3f and Fig. 4) the form figured by Naef is not like that shown by Jatta and Brock and certainly unlike that found by myself (Fig. 3f).

Actually the radula figured by Brock, Jatta and myself is distinctly less like that of the Teuthoidea than Naef's figure would suggest, though it is more like it than that of (*e.g.*) *Sepia*.

For the time being I do not think we are in a position to make a decision in the matter except to point out that, as the Argonautida are certainly not polyphyletic, the occurrence of these two types implies a very clear case of convergence on one or the other of the two types of Decapod radula.

Salivary glands are found in all the Octopoda, except *Opisthoteuthis*. They are subject to much variation in number and size, which is considered in detail on p. 30.

A crop is usually present, but it attains the form of a distinct diverticulum of the oesophagus only in the Heteroglossa and Ctenoglossa. In

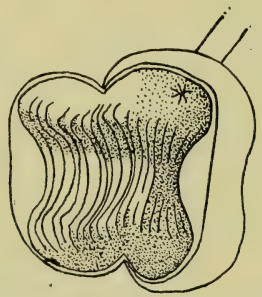


Fig. 6.—*Bathypolypus valdiviae*. Stomach. × 3.

the Vampyromorpha it is a mere swelling in the oesophagus and is absent in most of the Cirromorpha. The stomach is usually small and adapted for grinding, its walls being muscular and provided with a tough cuticle. A coecum is present into which the liver pours its secretion by two ducts. The liver is usually composed of a single lobe, but in *Chunioteuthis* it has a bifid extremity and in *Opisthoteuthis* it is double, as in some Myopsida (see p. 122). In some forms the initial part of the intestine is thick-walled and constitutes a kind of third stomach. The intestine is relatively short. There is usually an ink-sac; but it is absent in all the Cirromorpha and abyssal Heteroglossa. Pelseneer (1906, p. 303), apparently following a figure of Poli, suggests that the ink-sac is free from the liver in *Argonauta*, as it is in the Decapoda. I have not been able to confirm this suggestion. Anal valves are found in most forms, but they are not very conspicuous and are absent in some Cirromorpha.

*Respiratory Organs.* The general plan of the gill in the Octopodinae is described in Part I (p. 14), and, although that form is rather specialized, it may be taken as typical of most of the Octopoda as far as the identity of the parts and their general disposition are concerned. The detailed arrangement is, however, not the same in all the members of the order and some important deviations must be discussed.

(1) We may regard the gill (ctenidium) of *Nautilus* (Fig. 7A) as primitive in plan. It consists of two widely divergent rows of filaments, and the axis is shallow, consisting principally of the efferent and afferent vessels. The filaments are free and not attached to the surrounding parts. In all the Dibranchia they are attached to the wall of the mantle-cavity by their afferent edges. In the Decapoda (Fig. 7B) the filaments are still markedly divergent and the axis is tolerably shallow. Between the efferent and afferent vessels a cavity (the branchial canal) is, however, established, and beneath the gill the so-called branchial gland is developed. In the most specialized Octopoda (Octopodinae, Fig. 7D) the two lamellae

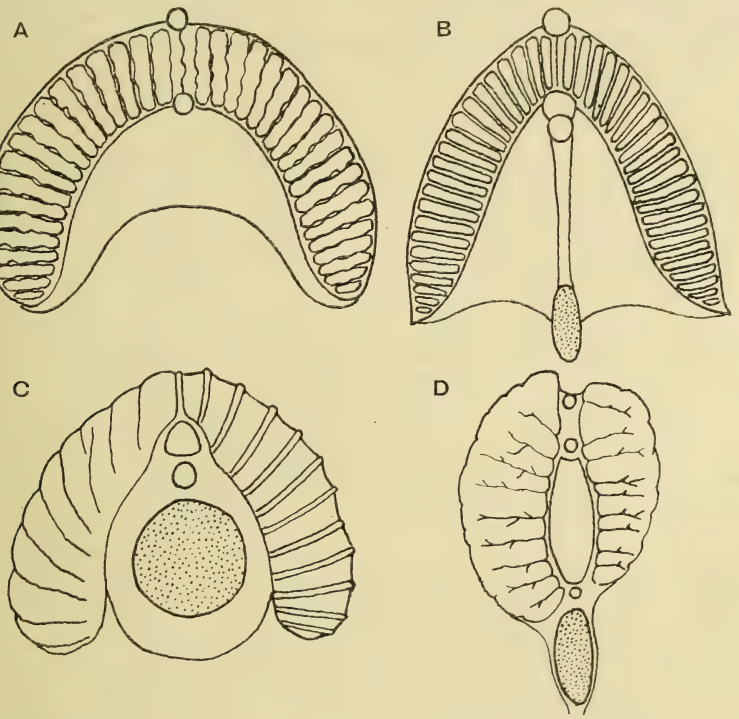



Fig. 7.—Transverse sections of gill in certain Cephalopoda.
(A) *Nautilus;* (B) *Sepia;* (C) *Grimpoteuthis* (Ebersbach) ; (D) *Octopus.* (Diagrammatic.)

have become parallel and attached to the branchial gland. A deep channel is developed between the lamellae (branchial canal), which is not quite like the branchial canal of the Decapoda, as it lies between the afferent vessels. The gill shows marked asymmetry owing to the reduction of the inner demibranch. In the Vampyromorpha, however, one infers from Joubin's account (1929, p. 381) that the gill is not of this compact form, but the filaments are divergent and not attached. In *Grimpoteuthis* (Fig. 7C) the filaments diverge widely and there is no trace of a branchial canal.

(2) In certain Cirromorpha a peculiar type of gill is developed in which the orientation of the filaments is quite different (see p. 123).

(3) In the Cirromorpha and abyssal Heteroglossa the gill is reduced

both in size and in the number of filaments. In the Ctenoglossa and *Vitreledonella* there is a progressive reduction of the inner demibranch leading to its complete disappearance.

*Nervous System.* The central nervous system in the Decapoda shows a certain amount of freedom of its constituent ganglia. The Vampyromorpha, to judge by the only form of which the nervous system has been so far studied in any completeness, show a similar lack of condensation. In the Cirromorpha, Argonautida and Heteroglossa the system is very much concentrated, all the chief ganglia being fused into a compact mass. For those who wish to relate the ganglionic fusion with increased functional activity (cf. Watson, 1930, Bargmann, 1929) this is a very instructive case, as no one would suggest that the Decapoda are inferior to the Heteroglossa and Argonautida in activity

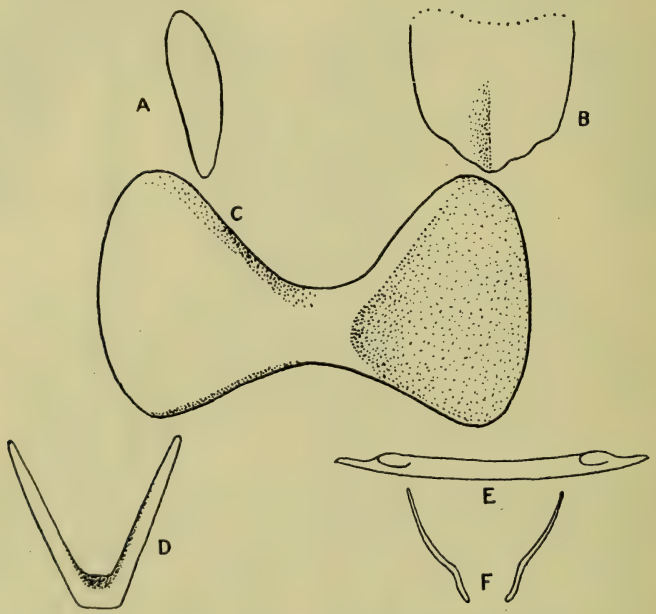



Fig. 8.—Diagrams of shell-vestiges of *Vampyroteuthis* (A); *Melanoteuthis* (B); *Cirroteuthis magna* (C); *Grimpoteuthis glacialis* (D); *Opisthoteuthis* (E); and *Octopus* (F).

or responsiveness, whereas (p. 189) there is an obvious difference in behaviour and degree of intelligence between the Argonautida and Heteroglossa.

*Sense Organs.* The chief sense-organs are eyes (p. 7), statocysts and olfactory organs. The Octopoda nearly all have two well-developed eyelids. This at least in the Incirrata has been regarded as an adaptation to life in turbid waters. In the Ctenoglossa, however (Chun, 1915, p. 519), the arrangement of the lid is exactly like that found in the Oegopsida.

The *statocysts.* Perhaps the most noteworthy feature is the absence of the isolated sensory prominences (*Zapfen*) which characterize the statocysts of the Decapoda and their replacement by a connective tissue

swelling (*Wulst*), (Hamlyn Harris, 1903, p. 340). In *Grimpoteuthis umbellata*, however, the prominences are found (Ebersbach, *l.c.*, p. 473). *Chunioteuthis ebersbachii* shows the normal Octopod structure. In certain Cirromorpha (*Chunioteuthis ebersbachii*, *Grimpoteuthis umbellata*, *Opisthoteuthis*) olfactory prominences like those of the Teuthoidea are found one on each side of the base of the funnel. In *Octopus* and *Eledone*, on the other hand, they are represented by sensory pits, as in the *Sepioidea*.

*Vascular System.* So far as is known this system is characterized by the persistence (? secondary acquisition) of large venous sinuses, which are replaced in the Decapoda by a true capillary system. However, in certain Cirromorpha (p. 124) an approximation to the Decapod system is found. Unfortunately the vascular system of few genera is known and no description is as yet available of the condition in the Vampyromorpha. The Ctenoglossa (p. 329) show the maximum development of lacunar spaces.

*Reproductive Organs, etc.* The Octopoda are, like all Cephalopods, dioecious. Well-marked sexual dimorphism is uncommon, except in the Argonautida. The question as to whether the Octopodinae are hyperpolygynous has been discussed in Vol. I (p. 16). The males seem to exceed the females numerically in the Argonautida (Pelseneer, 1906, p. 320).

*The Female System.* The ovary is apical in position. The eggs are large in the Cirromorpha and abyssal Heteroglossa, small in the Argonautida and in most of the littoral Octopodinae. The oviducal system consists of paired oviducts, spermoviducal glands and vaginae. The left-hand members alone are found in the Cirromorpha. The structure of the spermoviducal gland is not very well known. In *Tremoctopus* it is apparently tripartite (Sasaki, 1929, p. 31). The vagina is sometimes expanded to form a uterus. In *Ocythoë* (Sasaki, *l.c.*, p. 27) the water-canals seem to assist as gonaducts.

*The Male System.* This system is far more complex than in the female. The vas deferens is enlarged to form as many as three seminal vesicles and there are a number of auxiliary glands towards the distal end. These are more or less undifferentiated in the Cirromorpha and form part of the penial complex. In the Incirrata two of them (Needham's Organ and the prostate) are large and highly differentiated (Fig. 41). The spermatozoa are enclosed in spermatophores of varying shape, size and complexity. In some Incirrata these are reduced in number to a single one, which is of enormous size. In certain groups insemination is brought about by the hectocotylized arm, which is nearly always the third arm on the right side. This arm is autotomous and highly modified in the Argonautida. In the Heteroglossa its extremity forms a spoon-like organ. The process of insemination is not known in the Vampyromorpha, Cirromorpha and Ctenoglossa, and no trace of a differentiated copulatory organ has been found in them.* In some of these forms the males have enlarged suckers on the arms. This enlargement has also been noticed in the Heteroglossa and has been actually described as "hectocotylization", apparently by analogy with the *apparatus fixator* in certain Decapoda. Its use is, however, unknown (Vol. I, p. 21).

* For the occurrence of spermatophores in the Cirromorpha, see pp. 127, 138.

*Coelom.* The coelom is restricted to the genital capsule and the cavity containing the appendages of the branchial hearts. The two portions are in communication by the so-called " water-canals " or aquiferous ducts, which may be regarded as a part of the wide cavity of the Decapoda. The use of the canals as oviducts in *Ocythoë* is very interesting as it implies that what was originally an undifferentiated part of the coelom has assumed the rôle of the primitive coelomoducts. The obliteration of the pericardial coelom is carried still further in certain Cirromorpha (p. 126), in which one of the canals is partly atrophied, in *Tremoctopus*, in which they are both vestigial (Sasaki, 1929), and finally in *Argonauta*, in which they may even be absent.

*Skeletal Structures.* The central nervous system and otocysts are enclosed in a cartilaginous capsule. Other cartilaginous structures are found in the adhesive-apparatus (p. 8) and the gill supports of *Opisthoteuthis* (Meyer, 1906, p. 216). Branchial cartilages are said to occur in some Decapods, but have been found in no other Octopod. The fins of *Vampyroteuthis* and the Cirromorpha contain an endoskeleton of an elastic substance. Both Meyer and Ebersbach (Cirromorpha) state emphatically

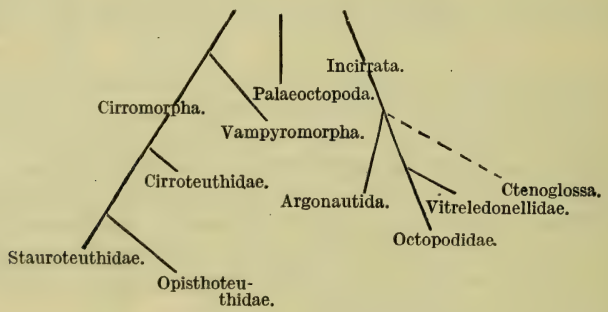



FIG. 9.—Diagram illustrating the probable lines of descent of the Octopoda.

that this structure is not cartilaginous. Brunnmüller (*Vampyroteuthis*) states that the similar substance in the fins of *V. infernalis* is composed of a " chordoid " tissue and is not cartilaginous. The internal *shell-vestige* of the Dibranchiata reaches its minimum development in the Octopoda. It is represented by a saddle-, hoop- or rod-like structure in the Cirromorpha and by two short lateral rods (dorsal stylets) in the Heteroglossa and *Tremoctopus*. Even these vestiges are absent in the Ctenoglossa, *Argonauta* and *Ocythoë*. The form of the organ in the Vampyromorpha is not very well known, but it is more or less rectangular and plate-like in *Melanoteuthis beebei* and elliptical and elongate in *Vampyroteuthis infernalis*.

The nature of the Octopod shell-vestige was established by Appellöf (1899, p. 1). His proof that it is a true conchostracal organ is two-fold. (*a*) The structure is developed from a " shell-sac." (*b*) It is chitinous (or chitin-like) and not cartilaginous. The first of these items is quite unexceptionable as evidence. As for the proof of the actual nature of the " corpus " of the organ I am not so certain. The substance is certainly

not cartilage. Appellöf and those who examined it subsequently, seem to have relied upon histological examination for deciding that it is chitinous. Actually I have found that the substance in *G. glacialis* gives a negative reaction to Zander's test for chitin (see "Microtomist's Vade Mecum," 1921, p. 507). Although we may accept Appellöf's verdict as to the nature of the Octopod shell-vestige, I think the matter requires further investigation, especially as in the Decapoda the fin-muscles are partly inserted into basal fin-cartilages and not (apparently) into the shell or its representative, as in the Cirromorpha.

## III. BIONOMICS.

*Habitat.*—Very little information is available concerning the habits and mode of life of the Octopoda and what is known concerns the Octopodinae (Vol. I, p. 19), Argonautidae and *Eledone* (s.s.). The Octopoda are, as already stated, an exclusively marine group. They are intolerant of low salinity and are very rarely found in water of less than 35 $^0/_{00}$. The Octopodinae (Vol. I), which are the only littoral forms, are sometimes found in estuaries and similar places, but they are regular inhabitants of such waters only if the latter are of normal marine salinity. Of the forms treated in this volume *Eledone* has been occasionally reported in water of low salinity, and I suspect that this may be true also of *Pareledone*, which is so common off the Antarctic continent. *P. charcoti*, *turqueti* and *polymorpha* (Robson, 1930*b*, *passim*) are found there in water of 33–32 $^0/_{00}$. *Graneledone setebos* was obtained in the inner recesses of the Ross Sea, where the salinity must be rather low, and specimens of *P. charcoti* and *turqueti* have been taken in McMurdo Sound. *Grimpoteuthis glacialis* was taken by the "Discovery" in 34–32 $^0/_{00}$, and *Cirroteuthis mülleri* (Davis Straits) was probably obtained in 30 $^0/_{00}$ or less. Everything, however, goes to confirm the impression that, "like the Amphineura and Scaphopoda among Molluscs and the majority of Echinoderms and Brachiopods (*e.g.*) among other groups, they seem quite incapable of living permanently in brackish water" (Vol. I, p. 19).

The vertical distribution of these animals and their general mode of life, *i.e.* whether they live on the bottom or in mid- or surface-water, is not easily ascertained. The majority of the Octopodinae (Part I, p. 19) live on the sea-bottom in shallow water. The Bathypolypodinae and certain of the Octopodinae are inhabitants of the lower reaches of the continental slope and are often found in very considerable depths. Our knowledge of the exact habitats of the rest of the group is far from complete.

The Vampyromorpha, Cirromorpha, Bolitaenidae and Vitreledonellidae seem all to be inhabitants of deep water. The Argonautida, though they are very frequently found at the surface, have also a wide vertical range. Abel (1916, p. 44 and foll.) and I (1926*a*, p. 1326) have pointed out that our knowledge as to the exact habitats of motile deep-sea forms is subject to very obvious limitations. Unless closing-nets are used we cannot know at what depth a specimen was actually caught, as it may have been captured at any point while the net was being hauled up. I have already (Robson, *l.c.*) given a short history of the use of closing-nets in relation to the study of abyssal Cephalopods, and it is only necessary here to point out that nearly all our deep-water forms have been taken in open nets or trawls. It follows therefore that from the actual process of capture we have very little exact knowledge as to the depth at which our recorded specimens lived, and must turn to less direct sources of information.

(*a*) We may collate all the records of a given species and ascertain

the minimum depth at which it has been taken. If a species or the members of a group have never been taken in water of less than 500 fathoms (*e.g.*) it is a fair inference that it is a deep-water form. As Abel (*l.c.*, p. 45) points out, it is very significant that scarcely any of the forms which we regard as abyssal were obtained in the early days of oceanic investigation, when only the shallower parts of the sea were explored.

(*b*) Although there is some danger of arguing in a circle, it is always suggestive of the abyssal habitat, if we find special adaptations such as enlarged or reduced eyes. Care should be exercised in this type of reasoning, as some adaptations regarded as peculiar to deep-sea animals may be shared by shallow-water forms inhabiting very muddy bottoms (Kemp, 1917, p. 233; Robson, *l.c.*, p. 1356; 1929, p. 2).

(*c*) If an animal is taken in a *trawl* worked at (*e.g.*) 1500 fathoms, there is, as I have said, always the possibility that it may have got in as the trawl was coming up. This is not, however, very likely, as several workers whom I have consulted have informed me that the contents of trawls used at great depths rarely contain mid-water or surface organisms. The fact that a given specimen was taken in a trawl at (*e.g.*) 1500 fathoms is evidence in favour of its having come from that depth.

(*d*) When we have reason to believe from analogy with littoral species whose habits can be observed, that we have to deal with benthic forms living on or just off the bottom and leaving it for brief excursions only, we may safely infer that the depth given is that at which they habitually live. Uncertainty as to the depth at which species live only affects those which are presumably inhabitants of mid-water.

It should be noted that forms known to live at great depths are sometimes found in shallow water. Sometimes this seems to be quite accidental as when single individuals are brought to the surface by currents (Straits of Messina, Abel (*l.c.*, p. 46)). Mortensen, however, (1929, p. 3) found off the Kei Islands " a very rich genuine deep-sea fauna in so shallow water as only 2–400 m., a condition with which only the Sagami Sea can compete."

Having thus seen the evidence by which we may determine the depth at which an animal habitually lives we have now to consider if we have any means of judging whether deep-sea forms live on the bottom or in mid-water.

(*a*) If (*e.g.*) shallow-water members of a family or genus are known to live on the bottom, it is, generally speaking, a legitimate inference that deep-water members of the same group will also live on the bottom. Thus, it is very likely that all the deep-water members of the Octopodidae are, like their littoral relatives, benthic. The criterion of systematic affinity, should, however, be used with discretion, as allied species sometimes have different habits.

(*b*) The attempt is often made to argue from structure to habits, but I do not think that the inference from structure can be safely utilized in dealing with this group, except perhaps as regards *Opisthoteuthis*, which is so unlikely to be a swimming or floating form, that one may be safe in asserting that it is benthic. I suspect that nearly all the Octopodidae are benthic, but it is quite possible that the large size of the web in the Bathypolypodidae may assist them in locomotion at a good distance from the bottom.

The argument from structure to habitat has been developed by Meyer (1906), Dollo (1912) and Abel (*l.c.*), whose views may be briefly summarized:

| | 1. | 2. | 3. |
|---|---|---|---|
| *Author.* | *Species or group.* | *Mode of life.* | *Proof assigned for* 2. |
| Meyer. | *Opisthoteuthis.* | Benthos. | ( ? General build). |
| Dollo. | *Cirroteuthis mülleri.* | Nekton. | Presence of fins (p. 129). |
| „ | *Opisthoteuthis depressa.* | Benthos. | Depressed form. Dorsal eyes (p. 133). |
| Abel. | *Cirroteuthis mülleri.* | Nekton. | Fins and web. (Funnel aborted) (p. 18). |
| „ | „ „ | ( ? Plankton). | Fins = " Balanzierapparat beim Schweben " (p. 105). |
| „ | *Cirroteuthis meangensis.* | Benthos (Burrowing). | Form similar to that of *Sepiola* (p. 55). |
| „ | " *Stauroteuthis* " } *S. syrtensis* } | Benthos. | Depressed body ( ? ) } Dorsal eyes } (p. 55). |
| „ | „ | ( ? Plankton). | Fins = " Balanzierapparat." |
| „ | *Froekenia clara.* | Plankton. | „ „ |
| „ | *Cirrothauma murrayi.* | Benthos (Burrowing). | Similarity to *Sepiola,* etc. (p. 55). Atrophy of eyes. |
| „ | " *Cirroteuthidae* " ( ? ). | Nekton. | Ventral position of funnel (p. 72) [ ? ]. |

There are several points to notice in this summary. (1) Abel, who treats *C. mülleri* as a nektonic form, rightly says (p. 26) that its swimming activity must be slight (on account of its semi-gelatinous consistency), and he also assigns to the fins the function of a balancing apparatus " beim Schweben." He is, therefore, in two minds as to whether it is really a nektonic form. (2) He thinks *Stauroteuthis syrtensis* is a benthic form and yet regards its fins as " balancers." (3) He compares *Cirrothauma* to *Sepiola*, *Rossia* and *Stoloteuthis* in body-form with very little justification, as the forms are most dissimilar. (4) The suggestion that *C. meangensis* is a burrowing form, made simply on account of a vague general resemblance to *Sepiola*, is valueless.

I have no doubt that the various views set forth above are quite possibly correct; but the evidence adduced is very slight, and Abel is evidently undecided as to whether the fins are used for swimming or digging or as balancers. The question whether the animals have a wide vertical range or whether they are merely sub-benthic, is left quite undecided. Abel is, I think, a little more fortunate in his treatment of the question whether the animals live in permanently lightless zones or in " euphotic " levels, and he makes the good suggestion (p. 55) that the eyes may be atrophied (*Cirrothauma*) because the animal lives buried in mud, although the presumed light-organs in this form are a difficulty here. All the same, I do not feel that there is a very safe argument from the size of the eyes to the general mode of life. *Opisthoteuthis*, which has very large eyes, is found in relatively shallow water. It may burrow in mud, but so on Abel's hypothesis does *C. meangensis*, and yet its eyes are not enlarged!

(*c*) Some slight assistance is to be had, if the stomach-contents are known. If the habits and distribution of the prey are known, it is possible to infer the feeding-habits of the captor, *e.g.* whether it feeds on or off the bottom.

(*d*) The total catch at a given station can be sometimes ascertained

(as *e.g.* from the " Challenger " volumes of summaries). " If a debatable form is taken with truly benthic animals it is a fair assumption that it also is probably benthic " (Robson, 1926, p. 1327). As I pointed out, however, this type of evidence is scarcely conclusive by itself.

On p. 82 I have tabulated all the recorded catches of Octopoda exclusive of the Octopodidae, and from these I think we can draw the following conclusions.

(1) *The Vampyromorpha.* With the exception of the single mangled fragment of *Laetmeteuthis*, which was found at the surface, and *Retroteuthis*, which is subject to a query, as Joubin gives a depth for it which is far from agreeing from the " Dana " Station List, none of these animals comes from less than 544 fathoms. The records of two are given as 0–750 and 0–1094 respectively. *Vampyroteuthis infernalis* (" Michael Sars," 51), *Melanoteuthis schmidti* (" Dana," 1261) and *Hansenoteuthis lucens* (" Dana," 1242, 1269, 1283) all seem to be mid-water forms, as they were all taken at depths less than that of the actual bottom sounded at the various stations. Subject to the possibility that some of them may have entered the net or trawl near the surface as it came up, I think we may conclude that these are bathypelagic, living in an average depth of about 1000 fathoms and probably having a fairly wide vertical range.

(2) *The Cirromorpha.* (*a*) The Cirroteuthidae and Stauroteuthidae. There are again no exact data except in the case of *Grimpoteuthis* sp. B (Robson), which was taken in a closing net at 790 fathoms. The majority have been taken in trawls at depths not shallower than 152 fathoms and averaging about 1000 fathoms or more. There are, unfortunately, no data by which we can estimate if they are benthic or mid-water forms, except one record of *G. umbellata*. This (" Michael Sars," 53) shows the specimen as caught in 1430 fathoms over a sounding of 1567 fathoms, *i.e.* 130 fathoms off the bottom (but cf. p. 18). The regularity with which these forms are taken in the trawl seems to suggest that they live on or near the bottom.

(*b*) The Opisthoteuthidae. These forms have been taken between 70 and 587 fathoms with an average of about 300 fathoms. There is no evidence as to the exact depth except the frequency of the capture by trawl. It has been generally held that their structure indicates a benthic habitat, and certainly the atrophied fins, flattened body and dorsal eyes suggest this. Nevertheless normal fins, erect body and lateral eyes (*Octopus*, *Sepiola* spp.) are found in benthic forms.

(3) *The Vitreledonellidae.* These are only known from five hauls in all. One (*V. translucida*) was trawled from relatively shallow water (0–125). Of the others one was taken in a trawl (" chalut ") at a very great depth, the other three in open nets in depths up to nearly 2000 fathoms. Were it not that *V. translucida* was taken in comparatively shallow water, one would have assumed that it was a truly abyssal form. However, as Abel (*l.c.*, p. 46) points out, deep-water forms are sometimes brought by currents up to the surface layers. *V. translucida* was obtained in a trawl in 0–125 fathoms, but it was on a ground very near the edge of the continental shelf and not far from soundings of 900–1200 fathoms.

(4) *The Ctenoglossa.* Only one specimen, *B. massyae*, was taken in a closing net and that in 1014 fathoms. The net was " towed just clear of the bottom." The members of the group have not been taken in less than 164 fathoms (one was " found on the shore after a storm "). The average

depth is about 1500 fathoms, obviously deeper than that reached by the other families of the group. *E. pygmaea* was obtained in a haul at 2949 fathoms and has the distinction of holding the record for depth among the Octopoda. There are few data as to the exact depth of their habitat. *B. massyae* var. *purpurea*, *E.* sp. (" Investigator," 393) and *Iapetella diaphana* (" Michael Sars," 56), were obviously taken off the bottom. The latter was relatively near the surface (164) over a great depth (1777). A few have been taken in trawls, but the majority are captured in nets. I assume that they have a wide range, but are mainly bathypelagic.

(5) *The Argonautidae.* There is overwhelming evidence derived from the older authors that these live at or near the surface. Nevertheless Orbigny (1840, p. 86) speaks of a diurnal migration from the deeper layers as characteristic of the " Philonexidae." Actually we know that *Tremoctopus* has been taken in a closing net at 1039 (? 1094) fathoms, and in a vertical net lowered to 1641 fathoms. *Alloposus* seems to live in rather deep water. Fragments are found at the surface very often, but the animal seems to live at about 200–300 fathoms. *Argonauta* has several times been taken in deep nets. I think it is very likely that these specimens entered the nets near the surface; but the members of the genus may have a wide range. At any rate *Argonauta*, *Ocythoë* and *Tremoctopus* must be regarded as characteristically pelagic.

The actual sort of bottom favoured by the benthic forms is only known in a few cases. *Eledone cirrosa* and *moschata* according to Vérany (1851, pp. 10, 14), Lo Bianco (1909, p. 646) and Jatta (1896, pp. 242, 247) both prefer muddy bottoms, and Lo Bianco suggests that *moschata* burrows in the mud. Orbigny (1840, p. 75), on the other hand, asserts that *moschata* prefers rocky coasts.

*Movement.* Most observers agree that the Octopodidae move quite rapidly by crawling on the arms as well as by the jets emitted from the funnel. Verrill (1882, p. 373) states that *Bathypolypus arcticus* swims also by opening and closing its web and that it was rarely, if ever, seen crawling. Orbigny states that *Eledone moschata* spreads its web out in swimming; but he may have seen something like the action observed by Verrill. Isgrove (1909, pp. 472–473) says that the web is not used by *E. cirrosa* for swimming, but only when sinking downwards. The large web of the Cirromorpha and Vampyromorpha may also be used for swimming. The locomotion of these two groups is uncertain and the function of the fins is unknown (whether used for swimming or balancing (cf. Abel (1916, p. 16) and this work, p. 20). *Argonauta argo*, according to the observations of Lacaze-Duthiers (1892, p. 48), did not use its arms in swimming, but " en contractant son sac " and by its funnel. Jatta (*l.c.*, p. 195), however, states that the arms are so used. Jatta (*l.c.*, p. 208) also asserts that *Tremoctopus* swims by means of the arms and web. As far as one can gather from Lacaze-Duthiers' observations (p. 41) *A. argo* has some special means of flotation, but his description is not clear.

*Food.* The Octopoda are generally exclusively carnivorous, although Massy (1916, p. 161) found in the gut of *Graneledone setebos* (" *Moschites* sp. ") a considerable quantity of seaweed. The animal was imprisoned in a rock pool, and Massy speculates as to whether its unusual diet was due to the absence of animal food or to old age. This, however, is an exceptional case. It has been assumed that the Cirromorpha are " micro-

phagous "; but this is merely an inference from certain structural features and is not in agreement with the only recorded facts as to the gut-contents. Scott (1910, p. 51) found in the stomach of *Grimpoteuthis* sp. the following Crustacea :—

*Trichopleon* ? *ramulosum.*
*Ilyarachna* or *Echinozone* sp.
*Nannoniscus* sp.
Amphipod gen. and sp. ?
*Andaniotes corpulentus.*
*Oithona* sp.
*Euterpe acutifrons.*
*Pontostratiotes abyssicola.*

Some of these forms are quite large (5–10 mm.). I found in the gut of *Grimpoteuthis glacialis* (1930*b*, p. 378) fragments of Polychaetes and it is quite likely that these animals feed on bottom-débris. The modifications of the gut, etc., of the Cirromorpha are discussed on pp. 29 and 120. Nothing is known of the feeding habits of the Vampyromorpha, Ctenoglossa and *Vitreledonella*. Among the Incirrata information is more plentiful. *Argonauta argo* feeds on small fish (Lacaze-Duthiers, *l.c.*, p. 54) and Crustacea (Lo Bianco, 1909, p. 645). The " Philonexidae " (*Tremoctopus* and *Ocythoë*) seem to devour Pteropods and Heteropods (Orbigny, *l.c.*, p. 86). Among the Octopodidae *Eledone cirrosa* lives on Crustacea and small molluscs (" coquilles ") (Orbigny, *l.c.*, p. 81). Isgrove (*l.c.*, p. 475) states that only crab remains are found in the gut of specimens kept in tanks. She mentions *Cancer pagurus*, *Portunus depurator*, *Carcinus maenas*, *Nephrops norvegicus* and " prawns or shrimps " as having been devoured. As it frequents lobster-pots it probably eats lobsters. Nordgård (1923) describes one eating a dead *Gadus*, and Isgrove suggests that it takes the mackerel used on lines for bait. The following is a record of some gut-contents of Bathypolypodidae which I have examined.

| | |
|---|---|
| *Bathypolypus arcticus.* | Thecosomatous Pteropods. |
| *Benthoctopus berryi.* | Crustacea (fragments), sedentary Polychaetes. |
| ,, *ergasticus.* | Polynoid Polychaetes, Crinoid fragments. |
| *Thaumeledone brevis.* | Crustacean, Polychaete } fragments. |

*Enemies.* *Bathypolypus obesus* has been taken from the gut of halibut (Verrill, 1882, p. 380). Isgrove (*l.c.*, p. 477) states that the only British records of *Eledone cirrosa* being eaten by fish relate to the ling and angler, and that the eggs of that form are eaten by crabs in aquaria. Probably in the adult stage Cetacea, marine Carnivora and large fish are the most important enemies. *Alloposus* seems to be preyed on by large marine Carnivora.

*Sociability, etc.* Although single individuals of the various species of Argonautida are often taken, and Lacaze-Duthiers (*l.c.*, p. 39) quotes Duvernoy to the effect that *Argonauta argo* is solitary, both Orbigny (*l.c.*, p. 86) and Vérany (*l.c.*, p. 44) state that *Ocythoë* and *Tremoctopus* are found in swarms. Isgrove suggests (*l.c.*, p. 471) that *Eledone cirrosa* may

live in small groups of two to six. *Pareledone polymorpha* and *charcoti* were taken in large batches by the "Discovery" (cf. Robson, 1930*b*, pp. 388 and 390) and may also be gregarious. As far as we know, the other members of the group are solitary.

*Miscellaneous.* From observations on animals in aquaria *Eledone moschata* (Vérany *l.c.*, p. 11), *Bathypolypus arcticus* (Verrill, *l.c.*, p. 373) and "*Philonexis*" seem to be mainly nocturnal and the other members of the group also may be more active at night. Vérany (*l.c.*) says that, although he kept *Eledone moschata* without food for ten days, he never saw any symptoms of "autophagy." Lo Bianco (*l.c.*, p. 646) records that an example in the Naples Aquarium devoured five of its arms. With the exception of *Eledone moschata* and *cirrosa*, which seem to tolerate captivity up to four months or longer (Isgrove, however, states that the health of *E. cirrosa* is very easily affected by captivity), none of the Octopoda seem to thrive in aquaria. Verrill (*l.c.*, p. 373) could keep *B. arcticus* for only four to five days and Lacaze-Duthiers' *Argonauta* lived for only fifteen days. Lo Bianco (*l.c.*, p. 645) found that the same species lives only a few days in captivity. It is a curious fact that Orbigny and Vérany both assert that *Eledone moschata* never discharges its ink when kept in aquaria. Isgroves states that *E. cirrosa* seems to lose the power of emitting the ink and its delicate health in captivity may be connected with the retention of the latter. According to Jatta (*l.c.*, p. 195) *Argonauta argo* quits its shell just before death. I have already (Vol. I, p. 22) commented on the habit that some of the Octopodinae have of entering hollow receptacles and of depositing their eggs in empty shells or other objects. Further facts on this subject are given on p. 25, and it remains here to point out that, like *Octopus*, *Eledone cirrosa* has the habit of entering hollow objects and that the male of *Ocythoë tuberculata* is often found in the branchial cavity of *Salpa* (Jatta (*l.c.*, p. 202), Lo Bianco (*l.c.*, p. 654), Naef (1923, p. 761)).

*Reproduction.* Nothing is known concerning the reproduction of the Vampyromorpha, Cirromorpha, Ctenoglossa and *Vitreledonella*. It has been assumed that the enlarged suckers seen in certain Cirromorpha (e.g. *Opisthoteuthis depressa*, Sasaki (1929, p. 11) and *Eledonella* (Auctt.)) are a sign of hectocotylization, though the male is not always thus distinguished (cf. *G. glacialis*, Robson, 1930*b*). *Vitreledonella* and *Amphitretus*, the Heteroglossa and Argonautida are all provided with a modified arm and coitus of some sort must occur in these groups. The absence of a modified arm and of spermatophores( ?) in the Vampyromorpha, etc., argues a different method of coitus from that found in the Incirrata generally. The functional significance of the enormous ligula and giant spermatophores found in some of the Bathypolypodidae is obscure. It is a curious fact that the giant spermatophores are single, and speaking generally one would assume that there must be some means of providing against unsuccessful discharge of a single spermatophore. The courtship and coitus of the Octopodinae have been discussed in Vol. I. There is very little known about these phenomena in other Octopodidae. More information is available concerning the exceptional phenomena seen in the Argonautida, in which the male is much smaller than the female. The elaborately modified hectocotylus in this group is autotomous and finds its way by independent movement to the aperture of the oviduct, after it is intro-

duced into the mantle-cavity of the female. The story of the discovery of the nature of the hectocotylus is well known and needs no repetition here.

The eggs of the Vampyromorpha, Ctenoglossa and *Vitreledonella* are unknown. Verrill (1882, p. 384) has described an ovarian egg of *Stauroteuthis syrtensis*. This was apparently wider than long (11 × 6 mm.) and had " a broad elliptical outline " when seen endwise, the two ends being truncated and smoothish, the sides ornamented with numerous regular roughened elevated ribs. The same author also described the eggs of an unknown *Cirroteuthis* containing embryos. These eggs were attached to Gorgonians, were covered by a firm transparent shell and measured up to 26 × 17 mm. (Verrill, 1884, p. 410). The following are the data I have collected on the size of eggs in other forms, the length of the eggs being reduced to a percentage of the mantle-length.

| | % |
|---|---|
| *Bentheledone rotunda* | 29 |
| *Eledone cirrosa* | 26 (av.) |
| ,, *moschata* | 24 ,, |
| *Thaumeledone brevis* | 22 |
| *Pareledone charcoti* | 17 |
| ,, *polymorpha* | 16 |
| *Thaumeledone gunteri* | 12 |
| *Pareledone turqueti* | 4 |

The eggs of unknown Cephalopods mentioned on p. 166 may be those of a Cirroteuthis. In *Eledone cirrosa* and *moschata* the eggs are laid in clusters (p. 263, Jatta (*l.c.*, pl. 7), Korschelt (1893, p. 69) and Naef (1928, p. 278)). The observations of Gravely on the method of deposition are alluded to on p. 269. It is not known whether *Eledone* has the same highly developed brooding instinct as *Octopus*. There is some evidence (Naef, 1928, tf. 123) that *Eledone* deposits the eggs on the shells of other Mollusca, a habit which I have already discussed (Vol. I, p. 22, and see p. 61).* Joubin (1888, p. 160) found that *E. cirrosa* will eat its own eggs when in captivity. The eggs of the Argonautida are, as far as we know at present, all small. Naef (*l.c.*, p. 71) gives the following measurements which must be taken, as he points out, as subject to some variation.

| | |
|---|---|
| *Argonauta argo* | 0·6 × 0·8 mm. |
| *Tremoctopus violaceus* | 0·9 × 1·5 ,, |
| *Ocythoë tuberculata* | 0·9 × 2·0 ,, |

The eggs of *Argonauta* are deposited in the secondary shell in which they are incubated. Those of *Tremoctopus violaceus*, which are laid in irregular masses, according to Kölliker (1844) are carried in the dorsal arms apparently folded in the web, an important observation, if we remember that the brood-shell of *Argonauta* is developed from those arms. From Naef's account (*l.c.*, p. 300) it seems that they are fixed to a solid

* Another example of the habit of depositing the eggs in the shells of other Mollusca may be added to the list. According to Wells (1928, p. 482) *Octopus rugosus* on the Florida coast deposits the eggs in empty " cockle " and " pearl oyster shells."

support secreted by the arms. The early development of *Ocythoë* is not known, but an observation made by Jatta led him to suggest (1896, p. 201) that it is viviparous. The eggs are provided with a stalk (Naef, *l.c.*, p. 296) which must, on this view, be functionless.

Joubin (1929*a*, p. 18) has recently made the interesting observation that the young of *Vitreledonella ingeborgae* are incubated in the mantle-cavity.

## IV. CLASSIFICATION AND EVOLUTION.

### (*a*) Introduction.

Very few attempts have been made to deal exhaustively with this subject, and indeed the lack of paleontological evidence makes the value of theorizing on the subject somewhat dubious. The first important work, and in some respects the best, is the essay of Brock (1880), " Versuch einer Phylogenie der Dibranchiaten Cephalopoden." In spite of his limited resources (e.g. *Cirroteuthis mülleri* was the only Cirromorph known to him), the essay is wide in its treatment and takes into consideration all the important organ-systems. Brock believes that the group is a highly differentiated one which had diverged from the Decapoda at an early date, but is related to the Ommastrephidae and *Loligopsis* (" Oegopsida "), that in some respects (*e.g.* muscular system) it is so specialized that its affinities cannot be detected and that probably the Argonautidae are the most primitive Octopoda. Various aspects of the problem were dealt with by Pelseneer (1888, p. 723), who ultimately concluded (1906, p. 331) that the order is descended from the Oegopsida " by the loss of the tentacles." Naef (1923, p. 795) thought that they were developed from an early Decapod type (? Aulacoceratidae) before the three main Decapod groups (Belemnoidea, Sepioidea and Teuthoidea) were differentiated. The special resemblance between the newly-discovered Vampyromorpha and the more specialized Decapod types was pointed out by me (Robson, 1929*a*), and I also indicated some of the main difficulties in dealing with Octopod phylogeny. Dollo (*l.c.*), Abel (*l.c.*) and I (1926*a*, *passim*) have attempted to correlate certain items of Octopod structure with the habits and distribution. Steinmann's theory that the Argonautidae and Ammonitoidea are closely allied (see also Schwartz, 1894) will be discussed later on (p. 61).

The discussion of this subject will be facilitated if we start by examining the characteristics of the deep-water forms. These are the most important part of the order and, although many of them are highly specialized, it is necessary to clear the ground by considering how far their various divergences are the result of adaptation to special conditions of life.

### (*b*) The Deep-sea Octopoda.

The adaptations of deep-sea animals have received a good measure of attention and are described in many text-books and other works. I have given an account (*l.c.*) of the special modifications of the abyssal members of the order here treated; but I think it desirable to revise that account critically, as we have to attempt to distinguish between the effects of convergence and the retention of certain archaic features in preparing our account of classification and evolution. Many of the animals described herein exhibit remarkable modifications, some of which are almost

certainly adaptive, while others defy our attempts to find such an explanation. Moreover, since my paper on this subject was published, we have received an important addition to our knowledge of the Vampyromorpha, one of the most important deep-water groups.

A. *External Parts.*

i. *Musculature and Integument.* All the Octopoda known to live at great depths have in one or another part of their structure some degree of muscular degeneration. The muscular tissue either becomes thin or may be actually replaced by gelatinous tissue. The various modes of degeneration were discussed by me (*l.c.*, p. 1331). I think this is the most frequent type of modification, although some deep-water Octopoda seem to be normal, e.g. *Grimpoteuthis glacialis* still exhibits powerful arm- and funnel-musculature.

The usual explanation of this modification, viz. that the gelatinous consistency of the tissues facilitates the admission of water which serves to minimize the external pressure, seems to me acceptable. However, we ought not to lose sight of the fact that the pelagic larvae of many surface forms are gelatinous or have thin musculature and that at least two non-abyssal genera of Decapods (*Grimalditeuthis* and *Leachia*) are gelatinous. As Abel says (*l.c.*, p. 52) " daraus ergibt sich dass wir aus der gallertighaütig Konsistenz des Körpers allein keinen Aufschluss über den Aufenthaltsort . . . gewinnen können."

ii. *The Web.* The Cirromorpha are distinguished by the very great depth of the web (p. 117). The web in the Vampyromorpha is well developed, but it rarely attains the great depth seen in some species of *Grimpoteuthis*. In the Ctenoglossa it is of moderate depth. Among the abyssal Incirrata it is moderately or poorly developed in *Vitreledonella*. Among the Octopodidae it attains a considerable depth in the Bathypolypodinae, though in other deep-water forms (e.g. *Benthoctopus thielei*) it is shallow.

It has been held by some writers that the expanded web is used as a net for capturing plankton, and it has been accordingly suggested that the cirri on the arms of the Vampyromorpha and Cirromorpha are used for sorting out or driving the food-particles thus obtained, towards the mouth ! Some Cirromorpha, however, feed on other food than plankton (cf. p. 23), and it is quite certain that a solid " net " of this sort would not capture any plankton at all, as it is now known that even open-meshed nets drive a large amount of plankton before them. It seems hardly likely that the animals float vertically and catch the plankton as it falls into the web. It is probable that the web is used in locomotion (see p. 22). In any case it is very important to notice that it becomes deep independently in the Cirromorpha and the abyssal Octopodidae. The convergent resemblance is suggestive of some identity of adaptation.

iii. *Mantle-Aperture.* In most of the Dibranchiata the mantle-cavity is in communication with the exterior by a wide transverse aperture. In the Cirromorpha this is represented by a small slit not much wider than the base of the funnel, and in *Chunioteuthis* it is conterminous with the aperture of the latter, so that the inhalant and exhalant currents enter and leave the mantle-cavity by the same aperture. In *Cirroteuthis*,

however, the aperture is tolerably wide, and in the Vampyromorpha, Ctenoglossa, *Vitreledonella*, littoral Octopodids and Argonautida it is widely open. In deep-water Octopodids it shows a distinct tendency towards closure, though the aperture is never as narrow as in the Cirromorpha. The closure of the mantle-aperture is not a phenomenon inseparable from the abyssal life, as neither the Eledonellidae nor Vampyromorpha (both deep-water groups) exhibit it. I am unable to make any suggestion as to its significance; but the wider problem of the associated modification of the respiratory and locomotor organs is considered on p. 57.

B. *Internal Organs, etc.*

(a) *Alimentary canal.* Though mandibles are present in all the members of the group, the radula is almost entirely absent in the Cirromorpha and is degenerate in some deep-water Octopodidae, e.g. *Thaumeledone.* It is well developed in the Vampyromorpha and in all the Incirrata, except those just alluded to. Surprisingly enough, it is well developed in *Vitreledonella*, in which, by reason of its highly modified alimentary canal (*q.v.*) and extreme delicacy, one would have expected it to be absent. I am a little uncertain as to how far the degeneration of the radula is restricted to abyssal forms. *Thaumeledone gunteri*, in which it attains the maximum degeneration short of complete disappearance, was obtained (a single example) from just over 200 fathoms. *T. brevis*, in which the radula is likewise degenerate, was obtained from 600 fathoms. Degeneration in a slight degree is seen in *Bentheledone rotunda* (1950 fathoms) and *albida* (1700 fathoms). The radula of *Grimpella* (shallow water) shows traces of degeneracy. On the whole, the definite instances of degeneration are found in deep-water forms, except in *T. gunteri*, the single known specimen of which may have been a straggler from greater depths.

The degeneration of the radula is not easily explained (see below).

The crop in the Cirromorpha is either absent or represented by a very weak enlargement of the oesophagus (*Cirroteuthis, Grimpoteuthis umbellata*). The only Vampyromorpha of which the alimentary canal is known are *Melanoteuthus lucens*, in his figure of which Joubin shows no crop, and *Vampyroteuthis*, in which Thiele mentions a crop-like expansion of the oesophagus. Among the Incirrata the crop is well developed as a distinct diverticulum, which is very large in the abyssal Eledonellidae. It is, however, reduced or absent in the Bathypolypodinae. As it is entirely absent in the Decapoda its absence in most of the Cirromorpha might be interpreted as an ancestral character rather than an adaptation to some special condition of existence. However, as the crop is present in *Cirroteuthis*, which is probably the most primitive Cirromorph, it seems clear that it has been lost in the other Cirromorpha. This modification of the alimentary canal is not easily attributed to differences in feeding between these abyssal forms and the surface types, and it is not found in the other two groups of abyssal Octopods.

The far-reaching modification of the alimentary system of *Vitreledonella* (p. 322) in which the salivary glands, oesophagus, crop and liver are all involved (the most striking being the reduction of the liver) are not accompanied by any degeneration of the radula.

I have observed no other feature in the main digestive tract that calls for comment in this connection. In certain Cirromorpha there is a " third stomach," but it seems to be restricted to that group.

The anterior and posterior salivary glands are interesting and their modifications may be tabulated as follows :—

| | *Vampyro-morpha.* | *Cirro-teuthis.* | *Chunio-teuthis.* | *Opistho-teuthis.* | *Cteno-glossa.* |
|---|---|---|---|---|---|
| Anterior. | ? | Very small. | Present. | Absent. | Both present. |
| Posterior. | ? | Absent. | Absent. | Absent. | Post. > ant. |

| | *Vitreledonella.* | *Octopodinae.* | *Bathypolypodinae.* | *Argonautida.* |
|---|---|---|---|---|
| Anterior. | Absent (?). | resemble Ctenoglossa. | Both present. | Ant. > post. |
| Posterior. | Median and unpaired. | | Posterior reduced. | |

It will thus be seen that the Cirromorpha show a very marked amount of reduction (cf. p. 122). Elsewhere there is definite reduction of the salivary glands in *Vitreledonella* and an insignificant amount in the Bathypolypodinae. I have very serious doubts as to whether there is any adaptive significance to be attached to these differences. The following additional facts make it amply evident that the absence or presence of the glands is not associated with any particular mode of life.

| | *Nautilus.* | *Oegopsida.* | *Myopsida.* |
|---|---|---|---|
| Anterior salivary glands. | Present ( ?). | Present, large. | Slightly developed. } Represented by unpaired intra-bulbar mass. |
| Posterior salivary glands. | Absent. | Present. | Present. |

*The Ink Sac.* This characteristic organ is entirely absent in the Cirromorpha and deep-water Heteroglossa (*Bathypolypus*, *Benthoctopus* and various " Eledonid " forms). It is found in the Eledonellidae ( ? somewhat reduced) and at least in one Vampyromorph (*Retroteuthis*). The explanation has been advanced that this loss is an adaptation, in that the organ is superfluous in lightless strata of the sea. If this is the case, it is very strange that it should be found in *Retroteuthis*, the Eledonellidae and *Vitreledonella*. *Retroteuthis* is equipped with light-organs and we must assume that it lives in lightless parts of the abyss, and we can hardly believe that the Eledonellidae * and *Vitreledonella*, which possess the ink-sac, perpetually live in some amount of light. Nevertheless the resemblance between the Cirromorpha and abyssal Heteroglossa in this respect is very striking. The loss of the ink-sac is the most frequent modification in the latter.

(b) *Respiratory Organs.* The gills in the Vampyromorpha appear to be normal in size and number of filaments. In the Cirromorpha two types of gill are found (p. 124), the more primitive of which shows little or no important difference from that of shallow-water forms. The more modified type (" half-orange ") is characterized by a marked reduction in the number of filaments and in the relative size of the gill itself. In the number of filaments the Eledonellidae do not differ conspicuously

* The Eledonellidae seem to be bathypelagic, but it is possible that they have individually an extensive range and may use the ink when near the surface. But (*a*) they do not figure in purely surface catches (p. 21), (*b*) their feeble musculature does not suggest that they are animals with a wide individual range. It is perhaps worth pointing out that *Iapetella diaphana* was once taken in a fairly shallow haul (164 fathoms, p. 89).

from the surface forms, but the size of the gill is reduced and the inner demi-branch is half as deep as the outer. These two modes of reduction are carried to greater lengths in *Vitreledonella* (p. 322), in which the inner demi-branch is entirely absent. Reduction in the size and the number of filaments is seen in the Bathypolypodinae.

As I have pointed out (1926*a*, p. 1352), the significance of the reduction of the gill is not clear. It might be held to be related to a generally lower metabolism characteristic of abyssal animals. A large respiratory surface might be unnecessary, if the organisms in question had indeed a lower metabolism. I do not know how far this explanation is complicated by the fact that oxygen is somewhat deficient in the deeper layers of the sea. Professor A. V. Hill, F.R.S., has kindly informed me that the availability of oxygen is probably not affected to any important extent either by low temperature or high pressure.

For the time being the reduction of the gills may be tentatively set down as an adaptation to abyssal conditions. It is noteworthy that there is no reduction in the single Vampyromorph, concerning whose gills we know something. There is always a possibility that the reduction in gill-size may be due to other causes. It is a little curious that there is a progressive reduction in the number of filaments throughout the Argonautidae and Octopodidae, the number falling from over twenty to under ten among surface and shallow-water forms. However, the transformation of the gill is not likely to be a " unitary " process.

(c) *Circulatory System.* Since writing my preliminary account of this subject (*l.c.*, p. 1342) I have not been successful in obtaining any material suitable for investigating the vascular system of the various groups. It remains to point out that the Stauroteuthidae (at least the two forms studied by Ebersbach, 1915, p. 441) resemble the Decapoda, in that the venous system is far more definitely vascular than in the Octopodidae, in which it is largely lacunar. Joubin (1924, p. 43) has found that in *Iapetella diaphana* the viscera are contained in a single enormous sinus, and I have noted the same in *B. massyae*. There is thus in one respect at least a noteworthy difference between two of our abyssal groups. Meyer (1906, p. 209) says that the Opisthoteuthidae (Cirromorpha) resemble the Octopodidae in this system.

(d) *Sense Organs.* The size and position of the eyes have been discussed by Abel (1916, p. 52 and foll.). As I have already pointed out (Robson, *l.c.*, p. 1350), there are curious differences in the size of the eyes of the abyssal forms. In the Cirromorpha they are small or moderate in *C. mülleri*, *G. umbellata*, *mawsoni* and *megaptera*, large in *G. pacifica* and *albatrossi*. In the Ctenoglossa and *Vitreledonella* they are small. The abyssal Octopodids show the same variation as the Cirromorpha; thus in *Thaumeledone* and *Bentheledone* the eyes are enormous, but in *Benthoctopus piscatorum* they are of normal size. In the Vampyromorpha they tend to be large. Special modifications are only seen in *Amphitretus*, in which the eyes are telescopic, in *Cirrothauma*, in which they are degenerate, and possibly in *Vitreledonella* (Joubin, *l.c.*).

Brauer (1908, p. 256) and Murray and Hjort (1912, pp. 680–685) have commented on the apparently idiosyncratic modification of the eyes in deep-sea animals. Murray and Hjort (*l.c.*, p. 680) evidently regard this idiosyncrasy as more apparent than real, and think that it is due to our

imperfect knowledge as to the penetration of sunlight and the occurrence of other sources of light in deep water. The whole question is complicated, as already indicated, by the likelihood that many benthic forms live in ooze, and by the known fact that blind forms, that permanently live in mud, occur in *shallow* water (*Bengalichthys*, *Typhlonarce* (Abel (*l.c.*, p. 55)). Without exact knowledge as to the depth at which our Octopoda live it is quite impossible to say whether the instances cited above are as anomalous as they seem to be. The statocysts are very much enlarged in *G. umbellata*, *Chunioteuthis ebersbachii* and *Opisthoteuthis*.

(e) *Reproductive System.* Such eggs of the Cirromorpha as are known are all large. In the abyssal Octopodidae they are similarly large. The size of the eggs, however, constitutes a very difficult problem, for, though it is possible that the large size may be an archaic feature (the eggs are very large in *Nautilus*), yet there is some evidence that the size is influenced by environment (low temperature). The following points are to be noted.

(1) All the "Eledoninae" have large eggs. The majority of these live in cold latitudes or deep water; but *E. cirrosa* and *moschata* occur in shallow water and in the Mediterranean, so that the large size of their eggs cannot be attributed to low temperature.
(2) Large eggs are laid by sundry Octopodids. Of these *Paroctopus* (Vol. I, p. 197), *Octopus fangsiao* and *globosus* (Sasaki, 1929) are mainly found in the cold waters of the N.E. and N.W. Pacific, but *Paroctopus digueti* occurs in S. California and oviposits in shallow water.
(3) The eggs of most of the Sepioidea are large and yet they are deposited in the shallow waters of warm seas.
(4) There is a certain amount of evidence that in cold water the eggs of other Invertebrates increase in size (Crustacea, Balss (1927, p. 951); Echinoderms (Mortensen, 1921, p. 249). The associated habit of incubation has been more frequently recorded in those groups and in Mollusca (cf. Burne, 1920, *passim*).
(5) In *Nautilus* the eggs are certainly very large, and yet it does not appear that they are deposited in very deep water.

(1), (2) and (3) certainly suggest that the environment is not the chief determining factor.

I do not think it possible, in view of the conflicting evidence, to say more than this, that the large size of the eggs may be dependent on their being retained for a long time in the vagina (which is used as a uterus), and that this in its turn is probably influenced by temperature and also by other factors. The incubation which leads to the large size of the eggs in shallow-water forms is probably due to local peculiarities of habit. I, therefore, believe that the large size of the eggs in the Cirromorpha and Bathypolypodinae may be due to the indirect effect of low temperature.

### (*c*) On Convergence in the Octopoda.

In attempting to determine the relationships of the various groups of Octopoda we are met with a familiar difficulty, viz. that of deciding whether certain resemblances are due to convergence or to relationship.

A work like this Monograph is not the place for exhaustive discussions on morphological principles. As, however, in preparing a classification of the group I have found it necessary to decide as to the extent to which sundry resemblances are due to convergence, I describe below the criteria used in arriving at such decisions.

I have not been able to discover an authoritative discussion * on such criteria. Convergence has been repeatedly discussed from one point of view or another, but this particular issue has never been exhaustively dealt with. Some vagueness actually exists as to the nature of the phenomena usually alluded to under the name "Convergence," and the meaning of the term "homoplasy" introduced by Lankester (1870) was (not unnaturally) confused by Osborn and others with that of "convergence." Although Osborn (1902, p. 264) admitted this and, to clear up the confusion, defined four different categories (Analogous Variation, Parallelism, Convergence and Homoplasy), his definitions are not always clear, as Willey (1911, p. xi) has already shown. Without embarking upon a lengthy discussion on these various concepts, I think that, for our particular purpose, the most important distinction we can recognize is between those resemblances which are not due to direct relationship but "result from independent functional adaptation to similar ends" (*id., l.c.*, p. 12) and those which are similarly not due to relationship and into which the element of functional similarity does not enter, or, at least, is not evident. By a legitimate extension of the concept we may include in the first category resemblances imposed on distantly related organisms by the action of similar or the same environmental factors ("epharmonic convergence"). It is not easy, of course, to say if the element of adaptation to a common end, or accommodation to similar environmental factors, is ever absent. It might even be claimed that these principles are at work in every case of convergence. I suspect, however, that there are a good many instances in which convergence is fortuitous, *i.e.* there is no evidence that it is due to functional or environmental similarity. It is difficult, for example, to believe that the resemblance between our Common Ram's Horn snail *Planorbis* (Pulmonata) and the Apple Snail *Ceratodes cornu-arietis* (Streptoneura) is due to identity of habit. It is worth while pointing out that Stephenson (1921, p. 117) and Parker (1931, in Press) both find that in certain groups of animals, convergence is due to the fact that the essential variations in a group and the resulting combinations of these variations are limited.

When two organisms belonging to (*e.g.*) different orders exhibit close resemblance in general facies or in particular structures and their habits and environment are identical, it is a legitimate inference that the resemblance may be due to similarity of adaptation and not to relationship. If, however, no such identity of habit can be shown, we are obviously thrown back on other criteria of the resemblance. (1) *Degree of resemblance.* Goodrich (1924, p. 145) points out that a resemblance due to convergence is *essentially superficial*, i.e. the similarity does not extend to all the parts of the structure involved. This is a useful criterion, but it is not absolute. Stephenson (*l.c.*, p. 122) does not believe that "a careful morphological examination, or a consideration of distribution,"

* Naef (1928) gives a very lengthy bibliography of works on morphological principles. I have consulted many of these for information on this subject, but without success.

will invariably suffice to distinguish groups of different origin. Degree of similarity may be (cf. p. 37) a matter of opinion, and sometimes two structures in remotely allied groups may acquire the closest histological similarity (*e.g.* the retina of vertebrata and that of *Pecten*). (2) *Degree of relationship between the organisms exhibiting similar structures.* When the organisms are very distantly related, *e.g.* when they are members of different phyla, this criterion is easy to apply. It is thus easy to decide that the tracheae of *Janella* (Mollusca) and of Insects have been acquired independently. When, however, the animals are more closely related, the matter is not so easy. Thus Willey (*l.c.*, p. 101) has described the relationship between two genera of Toads (*Myobatrachus* and *Rhinophrynus*) which "show several exceptional characters in common, side by side with a number of strongly divergent ones." It is instances of this kind that make the relationship of some of our Octopodid genera (below) so difficult to decide. (3) *Embryological history.* The status of a structure (*e.g.* whether it has been recently acquired) may sometimes be determined by its embryological history. This, in itself, is not a safe criterion (Wilson, 1895, p. 101). We are now so familiar with the modification of developmental history by special embryonic adaptations and the elimination of growth-stages, that it is not always certain that the absence of a given structure in the embryo is an indication of its absence in a phyletically earlier stage.

It has been suggested above that convergence may occur without any apparent identity of function, habit, or environment. When there are a number of points of resemblance in different organ-systems, the status of which (whether due to convergence or affinity) is uncertain and cannot be individually assessed by other criteria, and if no proof of identity of function or environment is forthcoming, we may reasonably believe that such resemblances are due to community of descent, as it is not very likely that a number of purely fortuitous resemblances would occur together in different organ-systems. This principle may be studied in the resemblances between the Vampyromorpha and Decapoda alluded to below.

### (*d*) Classification and Phylogeny.

### The Four Suborders and their Relationships.

Our knowledge of the various forms placed in the four suborders here recognized is not yet complete and in all probability some rearrangement will be necessary, *e.g.* when we obtain more information concerning the anatomy of the Vampyromorpha. Berry's *Laetmoteuthis*, which seems to have no cirri, full series of suckers and a highly differentiated radula, is at present placed in the Vampyromorpha, but, as far as it is known, it combines characteristics of the various suborders. The same is true of *Palaeoctopus*. The forms placed in the Cirromorpha are a fairly homogeneous group. The most dissimilar forms, such as *Cirroteuthis mülleri*, *Chunioteuthis ebersbachii* or *gilchristi* and *Opisthoteuthis*, share with one another a stock of common characteristics larger than their divergences. The homogeneity of the Incirrata is far more questionable, and I seriously

doubt the propriety of retaining in the same suborder such dissimilar forms as *Iapetella* and *Tremoctopus*, the divergences and common features of which are listed below.

*Differences.*

| *Iapetella.* | *Tremoctopus.* |
|---|---|
| Radula with multicuspidate teeth. | Radula with paucicuspidate teeth. |
| No shell-vestige. | Shell-vestige present. |
| „ adhesive-organs. | Adhesive organ „ |
| „ dorsal pores. | Pores „ |
| Suckers uniserial. | Suckers biserial. |
| Web, sectors more or less uniform. | Web highly differentiated. |
| Vagina moderate. | Vagina very large. |
| Spermoviducal gland small and (?) simple. | Spermoviducal gland large and tripartite. |
| No end-organ on third right arm. | An elaborate end-organ. |
| „ sexual dimorphism. | Sexual dimorphism. |

*Common Characters.*

No cirrhi.
„ fins.
Crop present.
No funnel-valve.
♀ ducts paired.

It will be seen that the differences easily outnumber the resemblances. The same is true of *Ocythoë* and *Octopus*. There is one circumstance, however, which induces me to retain the suborder for the present. If the divergences noted within the Incirrata were so correlated that we obtained two markedly divergent groups, there might be some reason for creating distinct suborders for, *e.g.* the Ctenoglossa and Argonautida. As it is, (*a*) the four Argonautid genera do not all differ in the same respect from the Ctenoglossa (thus *Tremoctopus* and *Iapetella* differ in the shell-vestige, but *Argonauta* resembles *Iapetella* in this respect), and (*b*) we do not as yet know the anatomy of the Ctenoglossa as well as we do that of the Argonautida. For this reason I am retaining the Ctenoglossa in the Incirrata, with the qualifications that there has been a great deal of evolution within the suborder and that in all probability it will be necessary to separate the Ctenoglossa as a suborder distinct from the Argonautida and Heteroglossa.

For some time now various authors have commented upon special points of resemblance between one or another group of Octopoda and the Decapoda, and two years ago in discussing the affinities of *Melanoteuthis* I suggested that the Vampyromorpha are the most archaic Octopods and resemble the Decapoda in several particular features. This question must now be carefully examined, and at the same time we must see if it is possible to determine the relationships of the various suborders. All the three larger suborders exhibit special resemblances to the Decapoda, which are tabulated as follows. It is very important to note that the three suborders resemble the Decapoda each in an almost entirely distinct set of characters.

The features mentioned in the following list are not necessarily found in all the members of each group. When they are only known from a limited number of genera, the latter are indicated in parentheses.

A. *Vampyromorpha.*

1. Presence of fins.
2. ,, ,, pedunculate suckers (*Melanoteuthis*, *Retroteuthis*, *Danateuthis*, *Watasella*).
3. ,, ,, funnel-valve (*Melanoteuthis*, etc.).
4. ,, ,, cephalo-pallial articulation of Decapod type (*Hanseno-teuthis*, etc.).
5. More or less homodont radula (*Melanoteuthis*, *Vampyroteuthis*).
6. Gill filaments free (*Danateuthis*).
7. Central nervous system diffuse (*Melanoteuthis*).
8. [Plate-like shell-vestige] (*Melanoteuthis*, *Vampyroteuthis*).
9. [Vestigial 5th pair of arms] (*Watasella*, *Melanoteuthis*, etc.).
10. No retractor pallii medianus (*Watasella*).

B. *Incirrata.**

i. Presence of cephalo-pallial articulation virtually of Decapod type (*Argonauta*).
ii. Gill-filaments very numerous (*Ocythoë*).
iii. Suckers on brachial membrane (e.g. *Ocythoë*).
iv. Absence or smallness of web (*Argonauta*, *Ocythoë*).
v. Radula (*Argonauta* = Sepioidea, *Ocythoë* = Teuthoidea, see p. 9).

C. *Cirromorpha.*

*a.* Presence of fins.
*b.* Position of stellate ganglion.
*c.* Olfactory prominences (*Opisthoteuthis*, etc.)
*d.* Intrabulbar salivary glands (*G. umbellata*).
*e.* Venous system (*G. umbellata* and *Ch. ebersbachii*).
*f.* Statocysts (of *G. umbellata*).
*g.* ♀ ducts single.
*h.* Gills of *C. mülleri* and *G. umbellata*.
*i.* Lack of adductor pallii medianus (*Cirroteuthis*).
*j.* Bilobed liver of *Opisthoteuthis* (? *Chunioteuthis ebersbachii*, *G. albatrossi*).
*k.* Absence of a crop.
*l.* Presence of branchial cartilages in *Opisthoteuthis*.

Now it may be argued that some or all of these characters resemble those of the Decapoda merely by convergence, and that they have no phylogenetic significance. It is thus contended (Naef, 1923, p. 726) that B iii is not a significant resemblance, and several authors have argued that the fins in the Octopoda are not homologous with those of the Decapoda. This is an argument to which careful attention must be paid. There is in the subordinate groups of the order much unquestionable evidence of convergence, and it may be true of the major groups.

* In addition to i–v, *Argonauta* displays a marked approximation to the Decapod muscular system in the weak development of the union between head and neck (Brock, *l.c.*, p. 211). I do not, however, feel certain that the latter should be treated as on the same footing as i–vi, as Brock clearly shows that, although the normal Octopod union is absent, it is replaced by a special system of muscular unions.

A 1. *Presence of fins.* Nothing is known of the embryology of the Vampyromorpha. According to Korschelt and Heider (1900, p. 264) the embryo of *Octopus vulgaris* at an early stage exhibits paired swellings "resembling in shape and position the fins described in *Loligo*." Judged by the normal criteria, this must be taken to suggest that the Incirrata are descended from finned ancestors and that probably the ancestral "Protoctopus" had fins. Though it may be held possible that the Vampyromorpha have lost the primary fins and re-developed secondary ones, the suggestion is gratuitously complex, and it is a fair assumption that it is unlikely. Brunnmüller (1929, p. 309) has recently shown that the fins of *Vampyroteuthis* resemble those of the Cirromorpha, so that the argument concerning the secondary nature of the fins of the Cirromorpha put forward by Dollo (*l.c.*) applies to the Vampyromorpha as well. He contends that neither in structure nor in position is the Cirromorph fin comparable with that of the Decapoda. (1) The structure of the fin is not exactly like that seen in *Sepia*, (*e.g.*) as it contains a mass of specialized supporting tissue. But in the Decapoda we are familiar with substantial modification of the fin-structure (*e.g.* in *Ctenopteryx*), and it is not unreasonable to suppose that two such structures fundamentally alike in origin may have undergone some measure of independent modification. (2) Dollo's argument that the position of the fins in the Decapoda and Cirromorpha is not identical, has little weight, as in the Decapoda the position of the fins varies very much (cf. *Spirula* and *Sepia*). On the whole, then, it seems a fair assumption that the fins are homologous in the two groups. At least their dissimilarity is not established.

A 2. *Pedunculate suckers.* Embryological evidence (cf. Naef, 1928, pl. 28) here seems to suggest that the peduncles are not homologous with those found in Decapod suckers. In *Octopus*, as in the Decapoda, the suckers arise as knob-like eminences on the arms and they are certainly not provided with definite peduncles. The minute structure of the peduncle of the Vampyromorph sucker is not known. All that can be said is that, when present, the peduncle is externally very like that of a Decapod. Perhaps it is best in this case to regard the homology as uncertain.

A 3. *Funnel valve.* There is no embryological evidence. The valve is identical in position with that of the Decapoda (at least in *Melanoteuthis beebei*) and it seems difficult to avoid concluding that it is homologous with it.

A 4. *Adhesive organ.* There is no embryological evidence. Joubin's description of the organ in the Vampyromorpha is not very detailed; but it does not seem to differ essentially from that of the Decapoda. It would be very remarkable if so characteristic a structure, involving two separate elements, were to have been independently acquired, and I believe that this is most unlikely.

A 5. *Radula.* There is no embryological evidence. This character has already been discussed (p. 10), and it was shown that at present we are unable to decide if the Vampyromorph type of radula is primitive or secondarily simplified.

A 6. *Gill filaments.* Up to the present the gill in only one Vampyromorph (*Danateuthis*) has been described and figured (Joubin, 1929, p.

381)*. It is not very easy to make out the exact structure from Joubin's figure; but it is quite evident that the filaments are " non réunies en un paquet serré " and that they are free at the extremities. The individual filaments are very much folded, as in the other Octopoda; but the absence of the basal union and (?) of the resulting branchial canal is certainly an archaic feature. Actually this gill seems to resemble that of a Decapod only in the absence of the basal union of the filaments. We need a fuller description before discussing it with any certainty; though I feel that one should note its possibly archaic character.

A 7. *Central nervous system.* There is no embryological evidence. It seems to me most unlikely that after having been very much condensed the system should secondarily (a thing unknown in the Mollusca) re-acquire such eminently characteristic features as separate brachial and superior buccal ganglia.

A 10. It is not possible to say whether this muscle has been lost or whether it was never developed.

On the whole, then, in default of overwhelmingly convincing proof, the bulk of the evidence seems to show that 1 and 3, 4, 6, 7 are primitive characters and not secondarily acquired. As for 2, although I admit that the embryological evidence is against the derivation of the Octopod sucker from a pedunculate form, nevertheless without some very strong evidence of similarity of function I find it hard to believe that such a specialized structure could have been independently acquired. For 8 and 9 see pp. 16 and 93.

As regards the Incirrata the position is as follows: B i and v have been already discussed and I need only mention that the adhesive organ of *Argonauta* is of a generalized type, in so far as it includes negative and positive elements on both head and mantle.

B ii. *Gill filaments.* The early development of the gills of *Ocythoë* has not been described. In *Octopus* (Naef, 1928, pl. 29, figs. 4–5) the embryo starts with three filaments and the number increases apparently to the adult figure. This might be taken as showing that the ancestral number was low and the high number in *Ocythoë* secondary. But in fact the embryo of a typical Decapod like *Sepia officinalis* shows but five lamellae (Naef, *l.c.*, pl. 17, fig. 5), and the number increases with age. No one would suggest, however, that the Dibranchiata are all descended from an ancestor with a few lamellae; some weight must be attached to the fact that there are numerous filaments in *Nautilus*. It is far more likely that the embryonic number is small in *Octopus* and *Sepia* as the result of developmental specialization.

B iii. *Position of the suckers.* In *Argonauta* and *Ocythoë* there is a clearly developed brachial membrane on each side of the arms, as in the Decapoda. Unlike the " Schutzsäume " of the majority of the latter, it is not free from the suckers but is united to the latter so that the suckers are incorporated in it. In its place of origin and depth it reminds one very much of the Decapod " Schutzsäume," but, its relation to the suckers being different, I think it may be regarded as an independently developed structure. In the embryo of *Argonauta* (Naef, *l.c.*, pl. 37, fig. 1) there are no membranes developed on the arms and one must assume that they were developed late in Decapod evolution. To derive the Argonautid

* Thiele's figure of *Vampyroteuthis* (1915) is not clear and his description is too brief to be of much use.

membrane from that of the Decapod or from a common ancestor having this structure seems inadmissible.

I admit that it may appear arbitrary to decide that there has been convergence in the position of the suckers and not in the character of the adhesive-organ. But the latter resemblance to a simple type of Decapod structure is remarkably close (Fig. 8) and is far more likely to be due to relationship. As regards the position of the suckers, what evidence there is (the embryological) is against the identity of the Decapod and Argonautid brachial membranes.

B iv. *Absence of web.* In the early embryo of *Argonauta* at least (Naef, *l.c.*, pls. 33–36) there is no web, and it is similarly absent in that of *Octopus* and the Decapoda. One may assume that the ancestral Incirrata had no web or a very low one, and that the condition seen in *Ocythoë* is primitive.

Thus we arrive at the same conclusion concerning the apparently archaic characters as we did concerning those of the Vampyromorpha. With the exception of iii they appear actually to be primitive. The primitive features in the Cirromorpha are less impressive. We have no embryological data to help us. C. *a* has been already discussed (p. 37). C. *b* The condition of the stellate ganglion in some forms is certainly like that of the Decapoda; but in view of the high specialization of the central nervous system as a whole I do not think there is much importance to be attached to it. C. *c*, *d* and *f* are such remarkable and characteristic features that they are not very likely to have arisen by convergence. C. *e* The situation here is very curious. In the Mollusca generally the system is primitively lacunar and this condition is found in *Nautilus*. The vascularization of the system in Decapods is a specialized condition possibly developed in relation to their great activity. This makes the similar condition in the Cirromorpha somewhat enigmatic, especially as in the Incirrata and Opisthoteuthidae there is a more lacunar system. C. *g* One of the female ducts seems to have been lost independently of the similar loss in the Myopsida. In all the other Octopoda the ducts are double and one can hardly believe that the common ancestor had a single duct or alternatively that the Cirromorpha and the rest of the Octopoda were derived from the Decapoda at different stages, the former after the loss of the female duct, the latter before that event. C. *h* The condition of the gills seen in *C. mülleri* and *G. umbellata* seems to be archaic. We can hardly believe that the Cirromorpha would be likely to re-acquire the generalized plan which resembles that found in *Sepia*. C. *i* It is difficult to decide whether this is a truly primitive condition. C. *j* If the embryological evidence and the condition of the liver lobes in *Nautilus* are to be taken as proving that the liver lobes are primitively separate, then in all probability the Cirromorph condition is primitive. C. *k* As is well known, there is no crop in the Decapoda. The more archaic *Cirroteuthis* has the vestige of a crop, and, as a crop is present in *Nautilus*, *Vampyroteuthis* and nearly all the Incirrata, I assume that the absence in the Cirromorpha is without a doubt secondary. C. *l* The gill in *Opisthoteuthis* is of the specialized "half-orange type." Meyer's description (*l.c.*, p. 216) of the cartilage is not very clear. It is plainly different from that of *Sepia* (Burne) and *Loligo* * (Williams), in

* In this form Williams describes (p. 64) the supports as of a chitinous nature ( ? as in some Lamellibranchs).

that there is a basal cartilaginous axis. It is not, however, clear whether the branches of the latter correspond to the filament-supports in the Decapods. On the whole I am inclined to believe that the branchial skeleton in *Opisthoteuthis* is a new development; but, if this view is correct, it is very remarkable that it is the most specialized type of Octopod gill that has re-acquired the Decapod-like branchial skeleton.

I think there is a final argument to dispose of in this connection. Were the Vampyromorpha, Cirromorpha and Argonautid Incirrata in any sense animals with a habitat and mode of life similar to those of the Decapoda, there might be some grounds for anticipating convergence in a number of organs of identical function. But the Vampyromorpha and Cirromorpha are obviously radically distinct from the Decapoda in this respect, and the Argonautida, though more active and vigorous, are probably not rapidly swimming, aggressive creatures like the majority of Decapods. When, therefore, we find close resemblance in a number of details not obviously referable to community of habit, our belief that the resemblance is due to community of descent is greatly strengthened. Finally, the actual number of resemblances is very high. I hardly think that so many similarities would be independently acquired without some strongly marked community of habit or environment.

The Vampyromorpha, in which the general facies is more primitive than in the Cirromorpha and Incirrata, may be treated as the most archaic Octopods. It must also be remembered that the plate-like shell-vestige must rank as a primitive character and that in all probability the " filaments " are homologous with an extra pair of arms. It is useless to inquire at present to which form of Decapod they are most nearly related. Certainly, if the above conclusions are correct, it was from a form in which the funnel-valve, adhesive-organ and possibly the radula had attained the same degree of development as we find to-day, *i.e.* it was a fairly evolved type. The question of the identity of the arms and the descent of the Octopoda from a tentaculiferous or from a ten-armed form seems to be an open one (p. 93), though it it is more likely that they came from the latter and so branched off the Decapod stock before the tentacles were evolved.

This derivation of the Octopoda from a fairly evolved Decapod type may seem surprising and may even encourage the suspicion that the resemblances, *e.g.* between the Vampyromorpha and Decapoda, are due to convergence. But I feel that it would be far more surprising were it to be proved that very close convergence had occurred in a number of small details without apparent identity of habit or mode of life.

A glance at pp. 92–112 will show us that beyond light-organs, somewhat enlarged eyes, dark coloration and feeble musculature the Vampyromorpha have acquired little special modification in relation to their deep-water habitat. It is a highly significant fact that, although this group is found in the deeper layers of the sea and may be regarded as sub-abyssal, they exhibit few specialized features. The gelatinous tissues and feeble musculature are found in other abyssal forms and may perhaps be regarded as a consequence of a bathypelagic mode of life. The light-organs certainly are to be treated as such. Without more knowledge as to the function of the cirrhi it is impossible to say if they subserve any

specialized activity peculiar to any particular habitat. Otherwise the structure of these animals, as known at present, presents us with none of the problems encountered in dealing with the Cirromorpha. The obvious token of a life spent in the deep sea which they bear in the light-organs, coupled with the widely-open mantle-cavity, the normal radula, gills and ink-sac, must prepare us for the possibility that the closure of the cavity, marked reduction of the gills and the loss of the radula and ink-sac in the Cirromorpha are not necessarily adaptations to abyssal conditions.

According to the theory of descent here offered the Incirrata are a less primitive stock, though still retaining some archaic features. These features are to a large extent different from those which persist in the Vampyromorpha. The Incirrata have very little in common with the latter, and must have branched off the early Protoctopodine stem at an early stage. The position of the Palaeoctopoda is discussed elsewhere (p. 113), and it is sufficient here to say that as at present known *Palaeoctopus* exhibits a mixture of characters of the three other orders rather than individual peculiarities.

The position of the Cirromorpha is more difficult to assess. The opinions as to the systematic position and phylogenetic status of these animals are very diverse, and hitherto no very satisfactory examination of the data has been made. Brock (1880, p. 284) considered that *Cirroteuthis* * was an early offshoot of the main Octopod stem. " Diese Form hat sich jedenfalls sehr früh vom Octopodenstamm losgemacht, wie die Beibehaltung der Schale und der Flossen, der Mangel des Mantelschliessers, welcher nicht etwas verloren ging, sondern nie erworben wurde, die Form des Gang.[lion] stellat.[um] und der Armnervenkommissur in diesem Sinne gedeutet werden muss " [sic !]. Pelseneer (1888, p. 736) also believed that *Cirroteuthis* was primitive, " certainement plus primitif que *Octopus*," though he did not produce evidence on this head. Naef (1923, p. 674), in his important Monograph (in which the Cirrata are not fully treated), evidently concluded that they exhibit a mixture of primitive and specialized characters. Pfefferkorn (1915, p. 522), who made an intensive study of the nervous system of the group, recognized traits of great specialization and some primitive features in the central nervous system, and thought they might be " eine Seitenfamilie der Octopoden, die sich . . . vielleicht auch von der Octopodenstammform abgezweigt haben." By stressing the fact that the concentration of the suboesophageal mass seems to exceed that of the Octopodidae, he appears to suggest that for " Octopoden " we should read " Octopodidae " and regard the Cirrata as developed from the ancestral type of that family. In attempting to explain the relationships of the Vampyromorpha, Cirromorpha and Incirrata (1929*a*, p. 485), I suggested that the Cirromorpha were a somewhat specialized offshoot of the main Octopod stem that branched off before the true Octopod (Incirrata) type was evolved. Meyer (1906, p. 262) thought that the Cirroteuthidae are more specialized forms of the Octopodidae. The features on which he relied for this opinion were : i. The reduction of the pericardium. ii. The single genital canal in both sexes. iii. The great expansion of the web. He held that it was hard to decide

* It will be remembered that very few species of *Cirroteuthis* were known when Brock was writing, and that the account given by Reinhardt and Prosch was all that was known of the anatomy.

how the radula came to be lost, and whether the absence of the ink-sac is due to loss or the retention of the primitive conditions (*Nautilus*), and whether the form of the male organs is primitive or specialized. Ebersbach (1915), who made a special study of two members of the group, evidently was disinclined to speculate on their origin and relationship. L. Dollo (1912, p. 130) showed no such diffidence. After a summary and rather superficial examination of the evidence he decided that "*Cirroteuthis* est un Octopode typique (= *Octopus*) adapté à la vie Nectique Secondaire" and *Opisthoteuthis* "est un *Cirroteuthis* specialisé pour l'adaptation à la vie Benthique (Tertiaire)" (p. 134). He examined six characters supposed to be indications of a more primitive status in *Cirroteuthis* and attempted to show that they were not primitive, and in addition cited seventeen features which he regarded as specialized. These will be alluded to in the following pages.

It will be as well to keep two things clearly before us in this discussion. (1) The forms included in the Cirromorpha are a fairly diverse assemblage. I think they are without any doubt a natural group and have many significant features in common. There are, however, some very noteworthy divergences, *e.g.* the occurrence of two forms of gill and shell-vestige and of genera with a completely closed mantle-aperture and others with it widely open. The median pallial adductor may be absent or present. This fact makes Dollo's discussion of the subject, which was based almost entirely on Reinhardt and Prosch's single study of *C. mülleri*, somewhat irrelevant, though actually *C. mülleri* is to my mind the most primitive Cirroteuthid. (2) Dollo, who was manifestly bent on proving that the Cirromorpha are specialized Octopodidae, includes in his list of specialized features the absence of the ink-sac, crop and spermatophores and the reduction of the suckers. Now in these and similar cases it is, as Meyer (*l.c.*, p. 263) points out, impossible to say offhand whether the absence or the reduced state of an organ is the result of atrophy or due to a rudimentary condition of development. Moreover, Dollo entirely overlooked the possibility that the ink-sac and crop might have been lost in two separate and remotely allied lineages. We may by contributory embryological or paleontological evidence be able to settle questions of this order. But on the facts of comparative anatomy alone it is often quite impossible to decide a question of this nature. I have tabulated below the various characters of the Cirromorpha under headings from which one may assess the morphological status of the group as a whole. The position assigned to each character is that deemed to be the most likely after the discussion on pp. 36 and foll.

1. *Characters presumed to be primitive in the Dibranchiata.*
   - *a.* Uniserial suckers.
   - *b.* Separate suboesophageal ganglia.
   - *c.* Open mantle cavity (*C. mülleri*).
   - *d.* Presence of fins.

2. *Characters resembling those of the Decapoda rather than those of other Octopoda* (*resemblance due to relationship and not to convergence*).
   - *a.* "Intrabulbar" salivary glands of *Grimpoteuthis umbellata.*
   - *b.* Position of the stellate ganglion (?).

*c.* Statocysts in *G. umbellata* (but not those of *Chunioteuthis*).
*d.* (?) Lack of *adductor pallii medianus* (*Cirroteuthis*).
*e.* Gills of *C. mülleri* and *G. umbellata* (Ebersbach).

3. *Characters resembling those of the Decapoda but resemblance probably due to convergence.*
   *a.* Venous system (Stauroteuthidae).
   *b.* ♀ ducts single.
   *c.* Absence of a crop.
   *d.* Branchial skeleton.

4. *Character presumed to be more primitive than the equivalent character in the Heteroglossa.*
   *a.* The shell-vestige larger than Octopodid vestige.

5. *Octopodid or "specialized" Octopodid characters.*
   *a.* Low number of branchial filaments.
   *b.* Condition of coelom (?).
   *c.* Condensation of central nervous system.

6. *Peculiar to the group.*
   *a.* Gills of "half-orange" type.
   *b.* Secondary web (*C. mülleri*, etc.).

7. *Specialization but uncertain from what ancestral form.*
   *a.* Deep web.
   *b.* Closure of mantle-cavity.
   *c.* Reduction of dorsal mantle-cavity.
   *d.* Loss of radula.
   *e.* Loss (?) of spermatophores.

8. *Shared with Vampyromorpha alone.*
   Cirrhi.

9. *Status uncertain.*
   *a.* Absence of posterior salivary glands (*G. umbellata* of Ebersbach a special case).
   *b.* Absence of ink-sac.
   *c.* ♂ reproductive system.

I think one fact emerges very clearly from this tabulation and that is the very heterogeneous assemblage of characters present in this group. It seems to have no decided affinities, and I think it actually is a highly characteristic assemblage of forms exhibiting a combination principally of Decapod-like and specialized characters. I certainly think that the Decapod-like characters preponderate and that those suggesting derivation from the Octopodidae are few. I am quite prepared to believe that animals undergoing a process of extreme specialization in which degeneration brought about the loss of certain characters, might very easily acquire a secondary resemblance to simpler ancestral forms. It is true that we do not know how many of the absences and simplifications in the Cirromorpha are due to degeneration. Three such characters require special notice here. It is usually held that the absence of the ink-

sac, crop and posterior salivary glands are due to loss. There is not much doubt that this is true as regards the crop (p. 39). As the ink-sac and posterior salivary glands are not found in *Nautilus*, we might assume that, instead of being lost in the Cirromorpha, they have never been developed. As far as the salivary glands are concerned, it is most likely that their absence is due to loss, as the glands seem to be progressively reduced in size and number and the highly evolved *Opisthoteuthis* has none at all. It is less easy to be certain about the absence of the ink-sac. The very general occurrence of this organ throughout the order (including the Paleoctopoda) makes it likely that it occurred in the primitive Dibranchiata and was possessed by the early Cirromorpha. Its absence is therefore likely to be due to loss. The question of the size of the eggs has already been discussed (p. 32).

The facts that force themselves on our attention are not, however, items in which loss is involved. The position of the stellate ganglion, the form of the gill in *C. mülleri*, etc., the statocysts of *G. umbellata*, etc., involve resemblances which are not likely to have been acquired by convergence. My belief, then, is that the view expressed by Pfefferkorn (*l.c.*) and arrived at independently by myself, is nearer the truth than any other. Brock and Pelseneer seem to be correct in their general view in stressing the primitive features of the group. Not only does the latter exhibit a combination of specialized features of unknown derivation with a rather high proportion of primitive and Decapod-like characters, but also it would be necessary to assume a remarkable amount of convergence with (*a*) the Vampyromorpha and (*b*) the Decapoda if they are to be derived from the Octopodidae. It is quite true that, if we treat them as a distinct suborder of independent derivation from the Protoctopodine stock, we have to assume a certain amount of convergence with the Incirrata, *i.e.* in the condensation of the nervous system, reduction of the gill and coelom. Nevertheless this is not nearly so much as we have to postulate on the hypothesis that they are specialized Octopodids. Exactly what importance we are to attach to the cirrhi, fins and uniserial suckers I cannot say. For the time being I think it likely that these, in common with the "Decapod" and other primitive features, indicate that they probably came off the Protoctopodine stock near the Vampyromorpha, but diverged from the latter at an early stage.

### Evolution within the Major Groups.

A. Some divergence is to be noted within the Vampyromorpha, *e.g.* the absence of the vestigial arms in *Vampyroteuthis* and of light-organs in *Watasella*. More noteworthy are the differences seen in *Laetmoteuthis*, which probably should not be retained in the Vampyromorpha, and in *Hymenoteuthis*. But it is not possible as yet to discuss these and other divergences, as the group is not well enough known.

B. The Palaeoctopoda obviously cannot be discussed as only a single specimen has been described.

C. Cirromorpha. As regards this suborder I do not think we need hesitate to distinguish three family groupings. I admit that, if we had more material and more anatomical knowledge, distinctions that now seem very obvious might be bridged over. There is, however, a very marked difference between *C. mülleri* and the other members of the group.

Its saddle-like shell-vestige, "Sepioid" gills, open mantle-cavity and absence of an *adductor pallii medianus*, as well as other features, are in most emphatic contrast to the structure of the majority of the species. It is true that several of the distinctive features of *C. mülleri* are found individually in other species. Thus the peculiar gill occurs in Ebersbach's *Grimpoteuthis umbellata*, the shell-vestige in *G. magna, hoylei* and *massyae*, and the highly specialized web in *Chunioteuthis*. The peculiar association, however, only occurs in *C. mülleri*. As this form departs so markedly from the other Cirrata, I do not hesitate to treat it as representing a distinct family. The next most marked divergence, i.e. *Chunioteuthis*, does not seem to differ from the other members of the Stauroteuthidae in enough characters to warrant our placing it in a separate subfamily. *Chunioteuthis* represents the most extreme phase of the evolution of the Stauroteuthidae, in that the pallial aperture and orifice of the funnel are confluent. *Cirrothauma* exhibits two completely discontinuous modifications of which no sign is, as far as we know, manifested in the other Cirromorpha, viz. the eyes are degenerate and the suckers are converted into light-organs.

The structure of *Chunioteuthis* gives us a very good example of the convergence so typical of this group. Indeed, if one had any doubts as to the occurrence of this phenomenon elsewhere in the group, the condition of affairs in this genus would serve to prove that it manifests itself in very remarkable ways. *Chunioteuthis* with its completely confluent mantle- and funnel-apertures, its "half-orange" gills and rod-like shell-vestige is obviously very distinct from *Cirroteuthis*, yet it has in common with the latter the very remarkable and highly specialized "secondary web." But, although it agrees with *Cirroteuthis* in the form of the web, it is very like the members of the Stauroteuthidae in most other respects. It seems to me that *Chunioteuthis* is either a Stauroteuthid which has acquired the secondary web by convergence (which would be very remarkable, as this form of web is very rare) or that it is a Cirroteuthid which has acquired several distinct Stauroteuthid characters similarly by convergence. We cannot escape from the dilemma by simply calling *Chunioteuthis* an "intermediate form," because in the bulk of its characters it is a Stauroteuthid. Lastly, if we treat it as a Stauroteuthid that has retained an ancestral form of web, we should have to assume that the simple web has been secondarily acquired in the Stauroteuthidae.

The series of modifications which we may trace in this group, end in a very marked departure from the normal Dibranchiate structure. The closure of the mantle-cavity, reduction of the number of branchial filaments, increasing depth of the web, increasing size of the eyes and the degeneration of the muscular tissues are all features which become progressively more marked. If I follow Ebersbach aright, a trace of the radula is still found in *Grimpoteuthis umbellata;* but otherwise the radula is entirely absent, and there is some measure of degeneration in the salivary glands. Many of these features are to be found in the Bathypolypodinae, and some of them are to be treated as adaptations to life in the deep sea (see pp. 27-32 and p. 59).

Finally, the architecture of the body in the Opisthoteuthidae has undergone one of the most striking modifications seen in the Cephalopoda. As already explained, the longitudinal axis has become very much shortened

and the animal is flat. The arms are short and almost completely involved in the web. In most particulars *Opisthoteuthis* exhibits Stauroteuthid characters developed to an extreme condition. Both pairs of salivary glands are absent, the gills are reduced to 3–4 filaments aside, the eyes are enormous and somewhat specialized, the fins are reduced and the shell-vestige has become almost straight, as though continuing the tendency seen in such forms as *Chunioteuthis gilchristi*. There may be a difference in the degree to which the venous system is vascularized (p. 31). Meyer (*l.c.*, p. 260) and Dollo (*l.c. passim*) both hold that *Opisthoteuthis* is adapted to a benthic life. Certainly the reduction of the fins would give one that impression. But the fins are reduced in *G. grimaldii* and yet there are no signs of other accommodation to a benthic life in that form. Flattening of the kind here observed has been noted among abyssal Echinoderms, *e.g.* in *Hymenaster* (Joubin 1912*b*, p. 218); but it also occurs among the littoral forms. Exactly how such a form can be regarded as an adaptation to benthic life I do not know. Certainly the littoral Octopodidae show no such tendency and the benthic and fossorial Sepiolidae are not built on this plan. Again, among the Echinoderms forms like *Rotula*, *Mellita* and *Clypeaster* and the Heart Urchins (*Echinocardium*) apparently live in mud and sand, yet the former are flattened and the latter erect. I believe the theory of Dollo and Meyer requires closer scrutiny and cannot be immediately accepted.

The relationships of the various forms placed in the Incirrata afford us a very interesting morphological and systematic problem. The unity of the group has been already discussed (p. 35), and it has been shown that it may be necessary to create a separate suborder for the Ctenoglossa.

I think there can be little doubt that of the three main groups the Argonautida are the most primitive. In spite of some obvious specialization (sexual dimorphism, autotomous hectocotylus) they exhibit individually certain traits which we have discussed (p. 38) and found to be primitive. These are found in the radula (*Argonauta*, *Ocythoë*), generalized adhesive organ (*Argonauta*), gill with many filaments (*Ocythoë*), Decapod-like funnel-organ (*Argonauta*) and moderate crop.* Neither the Heteroglossa nor the Ctenoglossa exhibit as many primitive traits.

As regards the relationship of the Argonautida and the Heteroglossa we may confidently assert that of the former the Alloposidae and Tremoctopodidae are most like the Octopodidae. The former are not so well known as the latter and may be disregarded for the moment. *Tremoctopus*, though possessing the characteristics of its tribe, resembles *Octopus* in its shell-vestige, radula, gills and adhesive organ. Are we therefore entitled to derive the Heteroglossa from the Argonautida through *Tremoctopus* or are the likenesses above mentioned between the latter and the Heteroglossa due to convergence? A glance at the following schemes will show us the possible course of events. Now the possibilities seem to be as follows (Fig. 10): (1) that the Heteroglossa are derived from a sexually dimorphic stock through *Tremoctopus* (A); (2) that *Tremoctopus* is the most primitive member of a dimorphic stock retaining ancestral traits in common with the Heteroglossa (B); (3) that the Heteroglossa and *Tremoctopus* have a common ancestry from a non-dimorphic

* For a discussion as to the status of the "sepioid" and "egopsid" radula (*Argonauta* and *Ocythoë*) see p. 9.

form, *Tremoctopus* having acquired its dimorphism independently of the other Argonautida (C); or (4) that the Argonautida are a homogeneous group and *Tremoctopus* has acquired its resemblances to the Heteroglossa mainly by convergence (D). For a satisfactory answer we must examine the three chief points of resemblances between *Tremoctopus* and the Heteroglossa each on its own merits. I do not believe that the occurrence of a paired shell-vestige in the two groups can be explained as a result of convergence. This explanation would necessitate (Fig. 10, D) the absence of the vestige in the ancestral Argonaut and its redevelopment in *Tremoctopus*, which having regard to the nature of the vestige, I think most

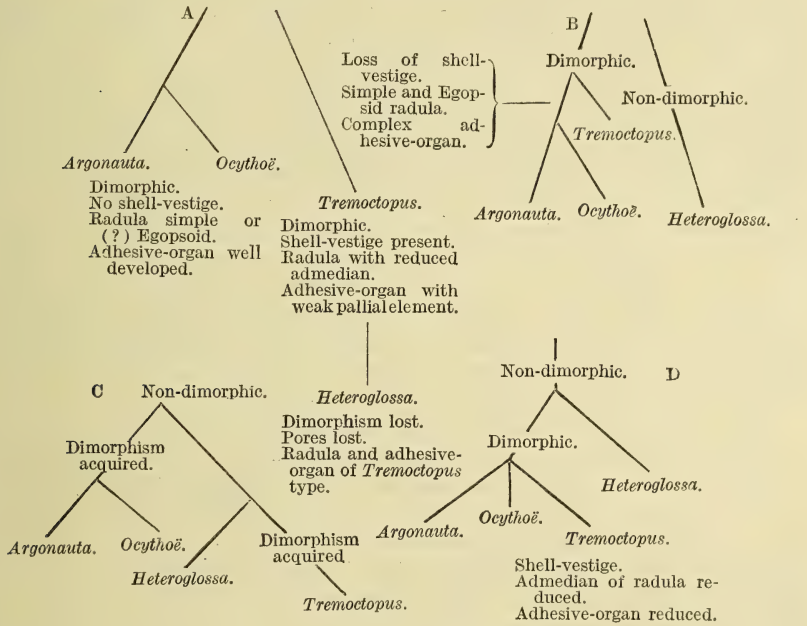



Fig. 10.—Diagrams illustrating possible relationship of the Heteroglossa and Argonautida (see pp. 46–48).

unlikely. We may, therefore, safely infer that its presence in *Tremoctopus* and the Heteroglossa is due to its having been present in their common ancestor, and that on scheme (D) its absence in *Argonauta* and *Ocythoë* is due to loss. But how are we to deal with the resemblances of the radula and adhesive-organ? If these are due to community of descent, it follows either that *Tremoctopus* and the Heteroglossa are closely allied and evolved as a group apart from the rest of the Argonautida, which does not seem likely, or else they have developed separately and the highly differentiated radula is archaic in the group and the condition seen in *Argonauta* is secondary. But although we may be in doubt (p. 10) as to the form of the Protoctopodine radula, it must have been either "sepioid" or "egopsid" and certainly not like that of the Heteroglossa. Have, then, *Argonauta* and *Ocythoë* re-acquired

archaic types of radula or has *Tremoctopus* come to resemble the Heteroglossa by convergence? To my mind there are two pieces of evidence that afford us a clue here. Firstly, *Argonauta* and *Ocythoë*, in spite of specialized features, both have other primitive traits. Secondly, the resemblance to the Octopod radula in *Tremoctopus* is rather generalized. The reduction of the admedian in the two groups is very striking; but the resemblance is otherwise not more than general, and it seems to me easier to believe that it is due to convergence than that, e.g. *Argonauta* and *Ocythoë* having originally had a radula with all its teeth differentiated and a degenerate admedian, re-acquired the primitive sepioid and egopsid facies. The argument in the case of the adhesive organ is rather similar. The organ in *Tremoctopus* is very like that of an *Octopus*, in that it has negative pallial and positive siphonal elements, but the pallial groove is far deeper and better developed than in *Octopus*, and I believe it quite possible that from a generalized type rather like that of *Argonauta* the same form may have arisen on more than one occasion. It thus seems likely that *Tremoctopus* and the Heteroglossa retain one ancestral trait (the double shell-vestige) and have acquired a resemblance independently in respect of radula and adhesive-organ. I believe that the view taken here is the least unlikely and makes the least demand on our credulity. Surprising as it is to find the amount of convergence here postulated, it would be still more surprising if (*a*) the Octopodidae were derived directly from specialized forms with marked sexual dimorphism like *Alloposus* and *Tremoctopus*, if (*b*) *Argonauta* and *Ocythoë* had re-acquired several archaic features by secondary modification, or finally (*c*) if the sexual dimorphism had been separately acquired in *Tremoctopus*.

The relationships of the Ctenoglossa and Vitreledonellidae are obscure. They are both specialized groups, particularly the latter, the alimentary canal of which has undergone a great deal of modification. *Vitreledonella translucida* has a sessile hectocotylus and a definitely Octopodid radula. In *V. richardi*, if Joubin's figure is correct (1924, pl. v, fig. 12), the radula is rather less like that of an *Octopus*. These animals may be specialized offshoots of the primitive Heteroglossate stock. The Ctenoglossa with their rather less concentrated central nervous system and highly specialized radula constitute a very difficult problem. In general they might pass for highly evolved Octopods in which hectocotylization, the adhesive organ ( ? in all forms), water-canals and shell-vestige have been lost, the crop enlarged and the gills modified, etc. The uniserial suckers, and absence of hectocotylus might, however, be considered as archaic. The tribe appears as a mosaic of some possibly archaic and other highly specialized characters and its systematic position cannot be adequately defined. Whatever position we assign them, they obviously have something in common with several groups.

On the whole, I think the Vitreledonellidae and Ctenoglossa should not be retained in the same tribe. The former agree with the Heteroglossa in the radula, hectocotylus and nervous system, and I think, are to be treated as bathyplanktonic Heteroglossa exhibiting very marked specialization especially in the alimentary canal. I have kept the Bolitaenidae apart as a distinct tribe (Ctenoglossa) because, although the habit, gelatinous consistency of the body and gill-reduction is like that of the Vitreledonellidae, and like the latter they have neither shell-

vestige nor adhesive apparatus, yet the differences in the radula, nervous system and hectocotylization are more striking and differentiate them at once from the Heteroglossa. They resemble the Heteroglossa in having a large crop and in the size of the posterior salivary gland. I admit, however, that the special resemblances between them and the Vitreledonellidae and other Heteroglossa are conspicuous.

### Octopodidae.

The Octopodidae are a large and numerous family containing 21 genera and probably over 200 species, for which I have retained two subfamilies. There are two main questions for discussion, (1) the validity of the divisions now proposed and (2) the inter-relationships in terms of descent, of their constituent genera. These may be dealt with concurrently.

The most outstanding feature of this family is, of course, the occurrence of a large number of deep-water or subabyssal species, the most highly modified of which I have placed in the Bathypolypodinae. These forms are distinguished by the following features.

(*a*) Loss of the ink-sac.
(*b*) Loss or reduction of the crop.
(*c*) Reduction of the gills.
(*d*) Reduction of the radula.
(*e*) Marked extension of the web.
(*f*) Large size of the eggs.
(*g*) Double funnel-organ.
(*h*) Large vagina.
(*i*) Large and few spermatophores.
(*j*) Narrowing of the mantle-aperture.
(*k*) Subgelatinous tissues.

Now, as already pointed out, many of these modifications, viz. (*a*), (*b*), (*c*), (*d*), (*e*), (*f*), (*h*), (*j*) and (*k*) occur collectively in the Cirromorpha and sundry isolated features are found among the Octopodinae. Thus *Macrochlaena* (Robson, 1929, p. 193) has a narrow mantle-aperture, reduced gill, deep web and double funnel-organ; *Paroctopus* has large eggs and *Hapalochlaena* has the ink-sac reduced and the web very deep. In *Benthoctopus* the ink-sac is completely atrophied. It is a noteworthy feature that the first three genera live in shallow water. *Benthoctopus* is principally a deep-water genus; but several species devoid of the ink-sac live in shallow water, or at least are only known from it at present (e.g. *B. magellanicus*). Similarly *Thaumeledone gunteri*, among the Bathypolypodinae, is only known from comparatively shallow water. It is as well, then, to bear in mind that the specialized features found in the deep-water Octopodidae and Cirromorpha occur also in a few shallow-water forms.

In the discussion (p. 43) on the Cirromorpha it was pointed out that three characters (the absence of the ink-sac and crop and the size of the eggs) might be regarded as ancestral and not the result of specialization. The same question might be raised with regard to these same features in the Bathypolypodinae.

(*a*) A crop is found in the Ctenoglossa, *Vitreledonella*, the Argonautida, Octopodinae, the Vampyromorpha and *Nautilus*, so that in all likelihood it was present in the ancestral Incirrata and has been lost in the Bathypolypodinae.

(*b*) An ink-sac occurs in nearly all the groups of Dibranchiata. It can hardly be claimed that the Bathypolypodinae represent a stage before the sac was developed in the sub-class.

(*c*) The size of the eggs in all probability is determined by circumstances of environment or habit (p. 32).

On the whole, then, I think it is safer to infer that the Bathypolypodinae are descended from the littoral Octopodinae than *vice versa*. Consequently we are led to a consideration of their peculiarities as adaptations to, or a consequence of, life in deep water. These have already been considered broadly in the section on "Adaptations" (p. 27), but some special comments are required here.

(1) *Loss of the ink-sac.* The loss of this organ is so capricious among deep-water forms (p. 30) that one is chary about asserting that it is an adaptation. If we could show that the Bathypolypodinae are ancestral to the littoral forms there might be some escape from the difficulties encountered in framing an adaptive explanation of this peculiarity, for the absence of the ink-sac might then be a primitive trait. However, this course is quite out of the question (see above), and we are left with the loss of the sac as a secondary feature. In the Heteroglossa it seems to be so inseparable from deep-water life that one must regard it as a consequence of the latter. Certainly (p. 49) the sac is lost in a few shallow-water forms; but its absence in these might be explained in the same way that Kemp (1917, p. 236) explains the occurrence of abyssal characteristics in certain shallow-water Crustacea, *i.e.* as adaptations to a life spent in water darkened by excessive silt. Nevertheless, it is a most curious fact that so many abyssal forms other than Heteroglossa have retained the sac.

(2) *Loss of the crop.*
(3) *Reduction of radula.*
(4) *Reduction of posterior salivary glands.*

} The reduction and simplification of parts of the anterior region of the alimentary canal in this group has not proceeded as far as in the Cirromorpha.

The reduction of the crop is very marked; that of the radula occurs definitely in only two genera (three species) and that of the salivary glands is relatively slight. The same process of simplification seems to be at work as in the Cirromorpha, but to be in a much earlier stage. This is a striking enough fact and evidently argues an important modification of the masticatory and digestive process in these forms and in the Cirromorpha. Again, however, the Eledonellidae, etc., do not show the modification. The Heteroglossa are certainly not "microphagous," as their stomach-contents include large fragments, so that the modification of the alimentary canal is not primarily due to their feeding on minute plankton organisms, as Abel (1916, p. 27) thinks.

(5) *Reduction of the gills.* The reduction of the gill seems to be closely connected with the abyssal life; though for the time being its functional significance is obscure. It certainly cannot be interpreted as an ancestral character (p. 38). It is perhaps a little curious that in the Octopodidae, as in the Argonautida, there is a tendency for the gill-filaments to be

reduced in littoral forms (cf. the difference between *Macroctopus* (14 filaments) and *Hapalochlaena* (6)).

(6) The increased *depth of the web* is not inseparably associated with the deep-water habitat (cf. *Macrochlaena*, Vol. I, p. 194, etc.), nor are all abyssal forms provided with such a web. Nevertheless it is of sufficiently frequent occurrence among deep-water forms to necessitate comment. No satisfactory functional explanation of the increase in depth can be offered, except that it may be supplementary to the funnel in locomotion.

(7) The double *funnel-organ* is in all probability not associated with any particular need or environment.

(8) *Closure of the mantle-cavity.* This, like (6), is not always found in deep-sea forms, though it is a noteworthy feature of the latter. I have previously suggested that in shallow-water forms it might be due to the necessity of keeping mud and silt out of the gill-cavity (Vol. I, p. 193), but I am now disinclined to maintain this view as the narrowing of the aperture, though restricting the intake of mud, would delay its evacuation. I now believe (p. 58) that the closure of the pallial cavity is associated with changes in locomotion and respiration.

(9) *Large vaginae.*
(10) „ *eggs.*
(11) „ *spermatophores.*

} Probably (9) and (10) are correlated and the size of the eggs (p. 32) would determine that of the vaginae.

The large size of the spermatophores, which attains its maximum in *B. ergasticus*, is quite inexplicable.

By way of summary we may say that in no instance is the adaptive value of these characters clearly shown. At least one character (7) seems definitely to be without such significance. The rest seem to be a consequence of lives spent in deep water, though the exact nature of the causal connection is obscure. Some of them are observable in shallow-water forms. In these instances they may be adaptations to peculiar local conditions analogous to those found in deep water. It seems impossible to avoid concluding that the Bathypolypodinae and Cirromorpha have acquired a marked resemblance to each other in certain special features as the result of convergence.

It finally remains to see what may be the relationship between the various genera of abyssal Heteroglossa themselves.

(1) Among the forms placed in *Benthoctopus* are some so closely resembling ordinary forms of *Octopus*, that, were it not for the lack of the ink-sac, one would place them in that genus. Moreover, some species of this genus tend to resemble shallow-water forms of *Octopus* that live in the same locality. Thus *B. magellanicus* and *eureka* are very like the local species of *Enteroctopus*. Sasaki compares *B. abruptus* with *O. tsugarensis* and *longispadiceus*. It looks as though some at least of these forms were independently derived from known littoral forms. It is very interesting that the absence of the ink-sac is the only sign of modification in *Benthoctopus*, although the species of this genus range just as deep as those of *Bathypolypus*.

(2) *The "Eledoninae."* The systematic history of this group is given on p. 257. It is necessary to discuss here whether the group is a natural one, *i.e.* whether the uniserial suckers and large eggs, which are the only distinguishing features, are sufficient grounds for retaining markedly dissimilar genera in the same subfamily. The status of the Bathypoly-

podinae has become part of this inquiry since the discovery (Robson, 1930*b*) of " Eledonine " forms whose general structure resembles that of the Bathypolypodinae. A rather long discussion on this subject is necessary. Although the outcome is somewhat negative, I think the status of these forms requires careful examination and the matter is not without interest.

For convenience' sake I have tabulated below the various distinguishing characters of the genera placed in the " Eledoninae."

| " ELEDONINAE." | 1. Hectocotylus. | 2. ♂ arms. | 3. Eggs. | 4. Ink-sac. | 5. Crop. | 6. Funnel-organ. | 7. Gills. | 8. Spermatophores. | 9. Vagina. | 10. Oviduct. | 11. Radula. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eledone* | no calamus present | heteromorphic | large | present | present | W | C 11–12 | small | small | long | normal |
| *Iodona* | calamus present | normal | ? | reduced | ,, | VV | 8 | ? | ? | ? | ,, |
| *Pareledone* | calamus present | ,, | large | present | ,, | W : VV | 7–11(?) | large | large | short | ,, |
| *Graneledone* | calamus present | ,, | ? | absent | (?absent) | VV | 5–8 | ? | ? | ? | reduced |
| *Bentheledone* | ? | ? | large | ,, | absent | ? | 5–6 | ? | large | short | ,, |
| *Thaumeledone* | ? | ? | ,, | ,, | ,, | VV : IIII | 4–6 | ? | ,, | ,, | degenerate |

It will be seen at once that this is a very heterogeneous assemblage. The only common subfamily characters are the uniserial suckers and large eggs. The differences between, e.g., *Eledone* and *Thaumeledone* and between *Pareledone* and the latter and even that between *Eledone* and *Pareledone* are very substantial, and certainly one's first impression is that *Eledone* and *Thaumeledone* should not be regarded as members of the same subfamily. In short, the four genera just mentioned seem to represent such marked divergences as to necessitate their separation and the treatment of the " Eledoninae " as a polyphyletic group in which the common characters have been acquired independently. On the other hand, there is something to be said for the retention of the group, and I think it best to state the arguments for and against this course.

### I. *The " Eledoninae " are polyphyletic.*

(1) The known genera present marked divergences *inter se*—

(*a*) *Thaumeledone*, *Bentheledone* and probably *Graneledone* agree in having no ink-sac, no crop, reduced gills, reduced or degenerate radula, deep web and a funnel-organ either **W**- or **V V**-like. They thus resemble *Bathypolypus* in many respects and differ very markedly from *Eledone* (s.s.).

(*b*) *Pareledone* differs from the *Bathypolypus*-like forms in being normally *Octopus*-like except in (1) arrangement of suckers, (2) size of eggs, (3) size of spermatophores and (4) size of vagina and oviduct.

(*c*) *Eledone* differs from normal *Octopus* in (1) and (2) and also (3) in its heteromorphous ♂ arms and (4) undifferentiated hectocotylus.

(*d*) *Pareledone* and *Eledone*, which are both different from the genera first mentioned in the characters given in (*a*), differ from each other in

(*c*, 3) and (*c*, 4) and also in the greater size of the spermatophores and vaginae in *Pareledone* and the smaller size of the oviducts.

(*e*) *P. nigra*, as far as we know it at present, differs from *Octopus* only in having uniserial suckers. Its radula is exactly like that of an *Octopus*.

(2) There is a general tendency among the Octopodinae to have a zigzag arrangement of the suckers, and in some individuals they become virtually uniserial. It is thus likely that the " Eledoninae " are made up of groups that came off the main Octopodine stem at different times and in different places.

II. *The " Eledoninae " are a homogeneous group.*

(*a*) The group occupies a more or less compact area (Fig 11). It is restricted to the Atlantic, Mediterranean, Southern Ocean and Antarctic waters. Outlying representatives are found on the east coast of Africa, the Kermadecs and off the west coast of S. America. It is absent from the north and east parts of the Indian Ocean and from Indo-Malaysian and Australian waters and from the Pacific generally (save for the west Colombian record) north of 30° S. I think it is certain that Rochebrune's *Eledonenta filholiana* (Fiji) is an *Octopus*. Roughly, then, it may be called an Atlantic-Antarctic group. It is to be noted, however, that it is not found in the Atlantic between about 30° N. and 22° S. except for Willemoes-Suhm's ambiguous record (p. 270).

(*b*) The uniserial suckers and large eggs, the only common characters diagnostic of the subfamily, are regularly correlated. (The size of the eggs is not known in all the species.)

(*c*) Though uniserial suckers are found sporadically as occasional variants in Octopod species, we have to do here with a character which occurs more or less regularly in all the known members of the various species. It is true that some of the species are only known from a single specimen. But *E. cirrosa* and *moschata* and *Pareledone charcoti*, *polymorpha* and *turqueti* are known from numerous to moderately plentiful series, and *Velodona* and *P. harrissoni* from 4–3 specimens apiece.

To one of these points special attention must be directed. Though the regular correlation of uniserial suckers and large eggs may suggest that the species exhibiting these features are a natural group, it might reasonably be asked whether the size of the eggs should be utilized in any discussion of this order. A very good case could be made out (p. 32) to show that there is a connection between either the environment or the habits and the size of the eggs. Thus it is likely that the size of the eggs of the deep- or cold-water species is determined by sea-temperature. The fact that forms like *E. moschata* and *cirrosa* in which the eggs are large occur in temperate seas and some of the forms of shallow-water *Octopus* which have large eggs (*l.c.*) are tropical, is not an obstacle to this view, as the size of the eggs in *E. moschata* (e.g.) may not be due to temperature but to some factor that leads to longer uterine life.

The arguments for and against treating the Eledoninae as a natural group might seem to us so equally balanced as to reduce the situation to an *impasse*. We are not much advanced towards a solution if we succeed in deciding whether the suckers are primarily or secondarily uniserial, though I think this assists us towards a clue. Naef (*l.c.*, p. 716),

FIG. 11.—DISTRIBUTION OF "ELEDONINAE."
(The approximate areas of distribution are indicated by the hatching.)

who was the first to suggest that this group might be polyphyletic, said that the uniserial suckers have been secondarily acquired. "Dafür spricht die alternative Anordnung am Grunde der Muskulatur der Saugnäpfe durch welche sie völlig regelmässig alternierend verschoben werden können." Nevertheless Guérin (1908, pp. 60–61), who made a complete study of the suckers, says that either condition might be derived from the other and that there is nothing in the adult structure to prove which is the original condition. Now all the evidence goes to suggest that the uniserial condition is archaic, and Naef himself (*l.c.*, p. 656) figures his ideal "*Protoctopus*" as having uniserial suckers and alludes (1928, p. 280) to the uniserial condition in the larval *Eledone* as the primitive one. The suckers in all known larval forms (Naef, *l.c.*) are uniserial. Moreover, in the archaic members of the group, the Vampyromorpha, they are uniserial, as well as in the Cirromorpha, Eledonellidae, Vitreledonellidae and probably some at least in the Palaeoctopoda.

I freely admit that in a somewhat exceptional developmental history, like that of the Octopoda, one might anticipate that the ordinary recapitulatory processes might be disturbed, so that the uniserial condition of the suckers in the embryo of *Eledone* might stand for very little. Nevertheless, in default of evidence that in the young the uniserial condition is a larval adaptation, I think we are entitled to hold that it is probably ancestral.

This question is complicated by the very marked degree of resemblance between *Thaumeledone* and *Bentheledone* (forms with uniserial suckers), and the Bathypolypodinae (biserial). Actually the position is as follows. The two groups resemble each other in the condition of the ink-sac, crop, gills, vagina, eggs and general habit. The radula of *Thaumeledone* and in a less degree that of *Bentheledone* shows a marked amount of degeneration, which is only suggested in the Bathypolypodidae. The suckers of the latter are biserial; those of the former are uniserial. Are the Bathypolypodinae a natural group and do *Thaumeledone* and *Bentheledone* belong to it, or have these two genera acquired the resemblance independently? Further, are the Bathypolypodinae descended from ordinary littoral Octopodines (biserial suckers), or are they descended in common with *Thaumeledone* from an ancestor with uniserial suckers acquiring their biserial suckers independently and apart from the Octopodinae? The situation is analogous to that which we met with in discussing (pp. 45, 47) the position of *Chunioteuthis* and *Tremoctopus*.

A glance at the table on p. 223 will show that on the whole the species placed in the Bathypolypodinae are a homogeneous group. Of course it is by no means out of the question that they are polyphyletic, but their general facies is uniform, the group as a whole differs in a number of well-marked features from the Octopodinae, and, what is more to the point, they differ very markedly from *Benthoctopus* in their far greater specialization, though they descend to no greater depths nor are they found more regularly in deep water. On the whole, then, I am inclined to think that they are a natural group.

Utilizing the only criterion available (viz. that of the number of characters involved), I think that *Thaumeledone* and *Bentheledone* are members of the Bathypolypodinae and that the latter are a natural group. Whether they have come from a stock with uniserial

suckers and their biserial forms (*Bathypolypus*) have acquired that arrangement independently from the Octopodinae, or whether the suckers are secondarily uniserial in *Thaumeledone* and *Bentheledone* I cannot say.

The plain fact is that there are in this family no clear-cut groups defined by regularly associated sets of characters. The really instructive point about this study is that, whatever arrangement is proposed, some measure of convergence must be postulated between the various groups. The systematist's difficulties are an eloquent testimony of the devious paths of evolution in this group.

Quite provisionally, then, I make the following suggestion. Following the embryological evidence I believe that the most likely course of events was that the ancestral Incirrate had uniserial suckers, that the biserial condition was independently acquired in the Argonautida and Heteroglossa, that the Bathypolypodinae, *Thaumeledone*, etc., are a natural group and *Bathypolypus* has acquired biserial suckers independently. I scarcely feel that the alternatives are likely, involving as they do either the assumption that in *Thaumeledone*, etc., the condition of the suckers is secondarily uniserial, or that all the groups are independently developed. I have already put forward the suggestion that the special resemblances that occur between the Cirromorpha and *Bathypolypus* are due to convergence. May I not seem inconsistent in claiming that similar tendencies among the Bathypolypodinae themselves are due to relationship and that the group is a natural one? The inconsistency, however, disappears when it is realized that the Cirromorpha and Bathypolypodinae are in many other respects very unlike each other, and that the points in which (e.g.) *Thaumeledone* resembles *B. arcticus* are very numerous and include some (*e.g.* the funnel-organ) which cannot be ascribed to adaptation or the direct effect of the environment.

Whatever be the truth in this matter I think that there has been a good deal of convergent evolution in this group. The divergences within the "Eledoninae" seem to loom larger than their resemblances, while the Bathypolypodinae seem to be a clearly characterized and natural group.

I have placed all the other *Octopus*-like genera in one subfamily, the Octopodinae. It is not easy to distinguish any other clear-cut groupings within the family. As pointed out in Vol. I (p. 4), the latter seems to be in a very active evolutionary state out of which very few well-defined groups have emerged. It is very interesting to notice that various genera (*Teretoctopus*, *Macrochlaena*, etc.) resemble the Bathypolypodinae in sundry characteristic features (deep web, loss of the ink-sac, etc.), and seem to represent stages in the development of that subfamily.

### (*e*) General Remarks on the Evolution of the Order.

(*A*) The most interesting and far-reaching modification which this order manifests is that of the respiratory and locomotor organs. As is well known, the current of water used for respiration is admitted through the mantle-aperture, and part, at least, is forcibly expelled through the

funnel as a locomotor jet. In the modification of this combined respiratory and locomotor system many structures are involved (adhesive-system, funnel, pallial aperture, gills, portions of the muscular system (median adductor, etc.) and possibly the web). I do not claim that the various parts and systems are simultaneously modified in every genus, but very marked changes in the capacity and closure of the mantle-cavity, in which the respiratory and locomotor systems must be involved, have taken place in the group and such changes are frequently correlated. Similar changes are seen in the Decapoda, though in that group they are not nearly so obvious nor are the respiratory organs so much modified. In the Octopoda the most important points to notice are as follows :—

(1) The locomotor system differs markedly from that of the Decapoda. In the latter there is usually a very efficient adhesive apparatus, no median adductor and no web ( ? locomotor organ). In the Octopoda the adhesive system is rather weak (except in *Ocythoë*) and there is a median adductor. The web appears (p. 22) to assume a locomotor rôle.

(2) In extreme instances the mantle-cavity becomes almost entirely enclosed. The closure is accompanied by reduction of the gills and of the mobility of the funnel. The forms which display these modifications tend to have a deeper web, and the adhesive apparatus is absent.

As I have already pointed out (1926*a*, p. 1336) the closure of the mantle-aperture must have a profound effect on respiration and locomotion.

(*a*) Owing to the narrowness of the pallial aperture there must be a reduction in the rapidity of intake of water and a corresponding slowness of evacuation of the waste fluids.

(*b*) For the same reason there must be a retardation in the rate of delivery of the locomotor jets from the funnel, as the water enters the mantle-cavity by a smaller aperture. At the same time it is possible that there is a gain of power, as the locomotor jet is concentrated in one place and the leakage through the mantle-aperture is reduced.

In the Dibranchiata generally there is a marked tendency for the mantle-aperture to be closed by the permanent adhesion of its free edge to the funnel, and it is desirable to tabulate the various manifestations of this process.

| | | |
|---|---|---|
| *Decapoda.* | Cranchiidae. | Permanent fusion of head and mantle approximately at the point of union of the adhesive-organ. |
| | *Grimalditeuthis.* | Permanent fusion of head and mantle approximately at the point of union of the adhesive-organ. |
| | *Symplectoteuthis.* | Permanent fusion of head and mantle approximately at the point of union of the adhesive-organ. |
| *Octopoda.* | Cirromorpha.<br>Abyssal Octopodidae. | Centripetal closure of mantle-aperture starting from its external corners. |
| | *Amphitretus*; cf. p. 219. | Fusion at three points ( ? Cranchiid and Cirromorph type of fusion combined) leaving two ventrolateral orifices. |

(3) The changes noted in (2) are principally found in deep-water forms. I do not pretend to understand the meaning either of the difference

between the locomotor systems of the Decapoda and Octopoda nor of the modifications involved in (2). What is interesting, however, is the intimate association of the changes in gill-structure and locomotor mechanism, which seem to me to be connected with a progressive reduction in the importance of the mantle-cavity culminating in the condition seen in *Opisthoteuthis*. I can only suggest that the branchial function is largely assumed by the external surface and the locomotor function by the web, and that these changes were initiated by life in deep water.

(*B*) The association of the respiratory and locomotor functions in the mantle-cavity and the suggested diminution in the importance of the latter leads us to an interesting speculation. It is a curious fact that a group of animals such as the Cephalopoda, which may be said (Vol. I, p. 22) to represent the climax of invertebrate evolution as far as strength, agility, size and intelligence are concerned, have never succeeded in colonizing fresh water and the land. The inability to live in brackish and fresh water is probably due to a physiological inadaptability, which is in sharp contrast to the readiness with which (*e.g.*) the Gastropoda have populated such waters. As far as the Octopoda are concerned, I believe a clue to the failure to colonize the land may be found in the functional association of the locomotor and respiratory organs. In complex animals like Cephalopods, a lung would be a prime necessity for terrestrial life. The pallial cavity which has adapted itself several times in the course of Gastropod evolution (Pulmonata, Cyclostomatidae, Littorinidae, etc.) to this function, has remained singularly unresponsive in the Cephalopoda, and I would suggest that, burdened as it is with a dual responsibility, it no longer possessed that power of accommodation that is found in the Gastropoda. The failure to develop a skeletal support for walking-limbs may have been a contributory factor in the inability of the Cephalopods to populate the land. In the Octopoda, however, the agility and power of rapid movement on land are considerable (Robson, 1925*a*, p. 2177), and I am not wholly convinced that the failure to develop limbs was a prime factor in their restriction to an aquatic life.

(*C*) The Octopoda include a number of groups which differ markedly in external facies and internal structure. The causes which led to the divergence of the Vampyromorpha, Cirromorpha, Ctenoglossa, Argonautida and Heteroglossa are very obscure, and it is not easy, as I have already said, to distinguish any corresponding divergence of habit or environment. Even if we recognize the limitations of our knowledge concerning the deep-water forms (p. 18) and confine our attention to those of which the habits are better known, we are in the same position. The Heteroglossa are mainly vigorous predatory creatures of benthic habits. The Argonautida are usually regarded as pelagic swimming animals (Naef, *l.c.*, p. 725); but *Argonauta* and *Tremoctopus* are probably not very vigorous and *Alloposus* must be virtually planktonic. Now the structure of these two groups does not give us, except in a few obvious and generalized items, the impression of definite and specific adaptation to the benthic and pelagic modes of life respectively. The saccular body of an *Octopus*, pliant and muscular, is no doubt well suited for crawling over irregular bottoms. The four genera of Argonautida differ very much among themselves; but the soft, flaccid body of *Tremoctopus* and

the gelatinous *Alloposus* are suited for a floating existence, and the more muscular *Ocythoë* may be a vigorous swimmer, though it is rather too saccular for rapid locomotion. Over and above these features I do not think there is a single item in their structure that distinguishes these groups as benthic and pelagic. For example, the outstanding features of the Argonautida, viz. the sexual dimorphism, incubatory habits, and remarkable hectocotylus, cannot be said to be, either individually or collectively, characteristic adaptations to a nektonic mode of life. I do not follow Naef (*l.c.*, p. 778) when he asserts " aus dem nektonischen Charakter ergibt sich auch die Notwendigkeit die Laiche mitzutragen." It is conceivable that the differences in the adhesive organ alluded to on p. 8 may be related to different modes of locomotion. But, in any case, the adhesive systems of *Tremoctopus* and the (benthic) Heteroglossa are very alike. Reference has been already made (p. 5) to the fundamental difference between the Decapoda and Octopoda as regards the suspension of the visceral sac. It is of some importance to note that a nektonic form like *Ocythoë* has the same kind of suspensory system as the benthic *Octopus*.

As regards the differences between the deep-water groups (Vampyromorpha, Cirromorpha, Ctenoglossa and Bathypolypodinae), some writers have endeavoured to relate them to differences in mode of life, etc. At first sight this seems a reasonable suggestion. Not only might some of these animals be benthic and others bathypelagic, but there is no doubt a very considerable amount of variation in the physical conditions in deep water, and, as Murray and Hjort (*l.c.*, p. 680) point out, the deep-sea environment is not nearly so uniform as was originally thought. Two examples will make this clear. (1) It is generally admitted that the diminution in sunlight is partly set off by the presence of light provided from organic sources (both from the dermal and other light-organs of animals and possibly from bacterial oozes). It is only on this ground that we can account for the presence of animals with normal eyes at great depths. (2) The decrease in temperature from the surface downwards, though regular in some places, is most irregular in others. Though probably more uniform than those at the surface, the conditions of life in deep water are probably varied enough to require marked differences in adaptation at various depths and in various places.

Although we do not know the exact habits of these animals nor in some cases the significance of given modifications, can we at least say that the various groups are distinguished one from another by groups of characters which collectively appear to be characteristic of different ways of life? When we find two groups as distinct as the Cirromorpha and Bathypolypodinae, which live in water of about the same depth, tending to resemble each other in a number of particulars which cannot be ascribed to relationship (loss of the ink-sac and crop, closure of mantle-cavity, size of web, modification of the radula), we are disposed to think that this is due to convergence and to infer that they live in the same environment. If at the same time we find that the Vampyromorpha and Ctenoglossa, which live at about the same depth as the others, do not exhibit these characteristics, our first impulse is to infer that they cannot be living in the same type of habitat. Thus the most obvious suggestion is that the Cirromorpha and Bathypolypodinae are adapted

to benthic conditions and the others live in mid-water. We may explain the fact that the Vampyromorpha have light-organs and the Ctenoglossa are without them, by suggesting that the former keep more regularly to the deeper layers. The general suggestion, however, is rendered very difficult to accept, if we consider that, although they resemble each other in several important respects, the Cirromorpha and Bathypolypodinae differ in certain structures in which the former agree with the Vampyromorpha. Thus the latter and the Cirromorpha have fins (balancing- or swimming-organs) and the Bathypolypodinae and Ctenoglossa (supposedly bathypelagic) are both without fins. If we interpret the absence of the ink-sac, as is usually done, in the Cirromorpha and Bathypolypodinae as an adaptation to lightless conditions, how is it that *Retroteuthis* (Vampyromorpha) which has light-organs (obviously an accommodation to lightless conditions) also has an ink-sac? Again, if the Cirromorpha and Bathypolypodinae have both lost the ink-sac as an adaptation to lightless or muddy conditions, how is it that so many Cirromorpha have normal eyes? If the Cirromorpha have lost the radula as the result of a "microphagous" or detritus-eating diet and the cirri are captatory or current-creating, on what do the Vampyromorpha feed which have a well-developed radula and cirri as well, and why have the feeble, short-armed Eledonellidae, which seem to be very ill-adapted for catching prey, such a formidable radula? Lastly we may explain the reduction of the gills in the Cirromorpha, Ctenoglossa and Bathypolypodinae on the general assumption that the gills are not necessary in abyssal animals of this kind on account of their low metabolism (p. 31). This will not explain (*a*) why some littoral forms have the gills reduced, (*b*) why *Vitreledonella* (p. 323) has undergone such excessive modification and (*c*) why there is among some of the surface-living Argonautida a very substantial reduction of the gill. Of course all these apparent paradoxes may turn out to be easily explicable in terms of habits and conditions as yet unknown. Moreover, our general conception as to the distribution of such factors as light, pressure and oxygen may be subject to much revision. One cannot help feeling, however, somewhat sceptical on this subject. The impression obtained from a general survey of the group is that, along with sundry obvious adaptive modifications, they manifest other changes which are neither the result of special adaptation nor of the direct effect of the environment, but innate tendencies of the group.

(*D*) The development of marked sex-dimorphism, of a highly specialized and autotomous hectocotylus and of brachial incubation in the Argonautida, renders that group highly interesting. Sex-dimorphism in size is not unknown in the Cephalopoda, and, as will be seen, there is a vague foreshadowing of the brachial incubation in the Octopodidae. The structure and use of the Argonautid hectocotylized arm are without parallel and appear quite discontinuously in the group. Whether these three separate phenomena are in some way correlated is unknown, and it is not easy to distinguish any circumstance in the animals' life in which one could hold that they are adaptive. It is true that not much is known of their behaviour. Naef (1923, p. 730) apparently holds that the series of specialization is as follows: *Alloposus*, *Tremoctopus*, *Ocythoë*, *Argonauta*, the latter being the most highly modified.

There are three separate elements in the remarkable incubatory phe-

nomena in *Argonauta*, viz. (1) the special use of the dorsal arms for the operation, (2) the fact that the membranes of these arms develop a shell-like brood-chamber, and (3) the resemblance of this " shell " to that of an Ammonite.

So far two theories have been put forward to explain the origin of the Argonaut " shell." (1) Steinmann (1925), impressed by the resemblance of this shell to that of certain Ammonites, suggested that the Argonautidae are really descendants of the Ammonites, which were in short Octopods and not Tetrabranchiates. This theory is concerned with the similarity of the Argonaut and Ammonite shells and does not account for the origin of the brood-chamber from the dorsal arms. (2) Naef (1922, p. 292 and 1923, p. 778) made the suggestion that " die Vorfahren der lebenden Argonautiden bemächtigten sich im reifen Zustand leeren Schalen, um darin ihren Laich abzusetzen. Diese wurde . . . an der Brutstelle mit Hilfe der Arme befestigt, wobei Sekrete von Hautdrüsen wirksam waren. Später hat die Absonderung dieser Drüsen die Vergrösserung des Brutbehalters selber ubernommen . . . Zuletzt diente das fremde Gehause nur noch als Kern für das selbsterzeugte und wurde schliesslich ganz entbehrlich . . . ich nehme also an, es haben sich die Urargonauten in leeren Ammonitenschalen gesetzt und sich denselben in der angedeuteten Weise angepasst."

Now there are a certain number of observations that lend support at least to part of Naef's theory.

(1) Several members of the Octopodidae are known to deposit their eggs in the shells of other genera of Mollusca. A description of this habit and a list of examples are given in Vol. I, p. 22, and this work p. 25.

(2) The web is used for cradling and supporting the eggs, even when the latter are deposited on a rock or stone (Vol. I, p. 22).

(3) *Ocythoë* has acquired the habit of entering and living in empty Salp cases (Jatta, *l.c.*, pl. vii, fig. 8; Lo Bianco, *l.c.*, p. 654; Naef, 1923, p. 761), and seems usually, when at rest, to bend the arms backwards to grip the case in almost exactly the same posture as the arms of *Argonauta*.

(4) *Tremoctopus* (Kölliker, 1844) seems to cradle the eggs in the web of the dorsal arms, the glands of which secrete a club-like support for the eggs. (See also Naef, 1928, p. 300.)

Three separate processes are involved here which must be carefully distinguished in discussing the theories as to the origin of the Argonaut " shell," viz. (1) oviposition in other shells, (2) the occupation of other shells or hollow receptacles (*Octopus*, *Ocythoë*), or the actual holding and cradling of shells containing the eggs, and (3) the incubation of the eggs, or cradling of them in the arms (*Octopus*, *Tremoctopus*).

It will be seen that some of the stages in the hypothetical history suggested by Naef are represented in the behaviour of the modern Heteroglossa. Actually the most crucial stage from Naef's point of view has not been recorded, viz. evidence that any Octopod cradles in its dorsal arms a shell in which it has deposited its eggs.

Steinmann's theory is, I think, satisfactorily dismissed by Naef (*l.c.*, p. 782). Though the superficial resemblance between the Argonautid and certain Ammonitid shells is quite remarkable, it must not be forgotten that similar resemblances may occur as the result of undoubted con-

vergence (cf. resemblance between shell of *Ceratodes cornu-arietis* and *Planorbis*). A more serious objection is the fact that there is no trace in the Argonautid shell of the typical Ammonitid structures (siphuncle, septa). Apparently in some Ammonites the siphuncle is very much reduced, but there is no evident fusion of the chambers. As for Naef's own theory, we have seen that there is evidence of a kind in support of it. According to the scheme of relationship suggested on p. 47, the Argonautida and Heteroglossa are collateral stocks, and one would say that the latter exhibit a series of ovipository instincts which is carried to a more extreme degree of development in the Argonautida.

Whatever we may think of Naef's theory as a whole, there is no avoiding the conclusion that the incubation of the eggs in a shell-like brood-chamber secreted by the first arms is the culmination of a series of stages in which (1) the dorsal arms become progressively more important in incubation; (2) a hard substance on which the eggs are laid is secreted by those arms, and (3) the habit of utilizing other shells is developed. I think, however, we ought to distinguish between (1) and (2) as opposed to (3). The use of the arms and their special secretory activity may be explained without invoking (3). We have, in short, some colourable evidence for believing that the development of a special solid substrate for the eggs may have developed in connection with the enhanced use of the dorsal arms. We have evidence that the eggs are deposited in a foreign shell, but no evidence that such shells are regularly cradled by the arms. We have also to consider the difficulty evidently felt by Naef that the earliest Argonaut shells are of Miocene date and the Ammonites become extinct at the end of Cretaceous times. In short, I believe that Naef's "Ammonite cradle" hypothesis is untenable. If we reject the "Ammonite cradle" we obtain no explanation of the assumption of a shell-like form by the secretion of the incubatory arms. The knobs and ridges of the "shell" may be due to the secretion being deposited along the line of the suckers, which, as Naef shows, fit into the knobs. But this does not explain the origin of a coiled Ammonitoid shell. I would therefore make the following suggestion. It is a well-known fact that in many Gastropods the operculum, which is secreted by the foot, is spirally coiled.* The arms of Cephalopods are homologous with the pedal area in other Mollusca and it is possible that they retain the capacity to reproduce spiral calcareous plates. In that case two spiral plates formed from apposed velar expansions and joined in the middle line might very well produce a structure simulating an Ammonite shell, the secondary ornamentation being, as already suggested, due to the presence of the suckers.

### (*f*) Summary.

#### A. *General.*

(1) The criteria by which resemblances due to convergence may be distinguished from those due to relationship are discussed (p. 32), and numerous instances of convergence in the Octopoda are described. They may have arisen in at least one instance (Cirromorpha and Bathy-

* It is as well to remember that the operculum is not always spiral but may be concentric, imbricated, etc. It is, however, primitively spiral (Pelseneer, 1906, p. 73).

polypodinae) as the result of the occupation of a habitat (the deep sea) in which special adaptations were called for. This is not easy to prove (p.59), but it is possible. In the majority of instances they cannot be explained in this way, and are more likely to be due either to innate and quite fortuitous (p. 60) tendencies or to the fact that the existing Octopod genera are the survivors of a larger series of groups in which (as was suggested for the species of Octopodinae, Part I, p. 4) a number of characters was combined again and again in very different groupings (in the absence of strict physiological and other bars to intercourse), so that the same character appeared more than once in dissimilar groups.

(2) The following features seem to be characteristic of deep-sea Octopods—(1) gelatinous tissues, (2) deep web, (3) narrowing of the mantle-aperture, (4) reduction or loss of the crop and radula, (5) loss of the ink-sac, (6) reduction of the gills, (7) enlargement of the eyes, and possibly (8) increased size of the eggs. The utility of (1), (6) and (7) and possibly of (5) is held to be established. The others may be adaptive, but their utility is not clear. Some of these features occur in shallow-water species (p. 49).

(3) Naef's theory as to the origin of the Argonaut " shell " is examined and rejected and a new explanation is proposed (p. 62).

(4) The mantle-cavity in the Cirromorpha and Bathypolypodinae undergoes a progressive enclosure and reduction in size. Concurrently with this process the organs of siphonal locomotion and of respiration, which make use of the same current admitted into the mantle-cavity, undergo a more or less correlated modification. It is suggested that the web and general integument take over the chief work of locomotion and respiration (p. 57).

(5) The adaptation of the various groups to distinct modes of life is discussed (pp. 18, 27, 58). Due allowance is made for the lack of exact information as to habits and distribution (p. 18), but doubt is expressed as to whether the main structural divergences can be associated with habitudinal differences (p. 60).

(6) As compared with the Decapoda and various orders of Gastropods and Lamellibranchia, the Octopoda are a small order and are (except for the Octopodinae) possibly in a moribund condition. The question as to why such highly-organized animals have never obtained a footing in fresh water or on the land is discussed (p. 58).

(7) The chief feature in Octopod evolution is their repeated invasions of deep water. Over half of the described genera come from water of over 500 fathoms in average depth.

(8) Although (*a*) the Cirromorpha are highly specialized in many respects and (*b*) the Argonautida exhibit many archaic traits, it would be correct to say that the more archaic members of this order are inhabitants of deep water, and that in part, at least, the old belief in the antiquity of the deep-sea fauna is justified, as far as the Octopoda are concerned.

### B. *Special.*

(1) The Vampyromorpha (as far as they are known and with the possible exclusion of *Laetmoteuthis*) and Cirromorpha are probably homogeneous and natural groups (pp. 35-46). The marked difference

between the Ctenoglossa and certain of the Argonautida (p. 35) suggests that the Incirrata may have to be divided into two suborders.

(2) The three chief suborders resemble the Decapoda in a number of special features, and it is suggested that they branched off the main Decapod stem after the latter had developed certain characteristic features (funnel-valve, pallio-siphonal adhesive-organ, fins, etc.), but before the radula was much differentiated and before the development of tentacles.

(3) The Vampyromorpha are probably more archaic and less specialized than the Incirrata and Cirromorpha.

(4) The special characters regarded as homologous with the similar characters in the Decapoda are: (1) fins, (2) funnel-valve, (3) adhesive-apparatus, (4) gill with small branchial canal and divergent filaments, (5) low web, (6) intrabulbar salivary glands, (7) statocysts equipped with sensory knobs, (8) liver in two parts. The following resemblances are probably due to convergence: (1) brachial membranes, (2) single female ducts, (3) branchial cartilages of *Opisthoteuthis*, (4) absence of crop. The nature of the resemblances in the following is uncertain: (1) pedunculate suckers, (2) completely vascularized venous system, (3) absence of the *adductor pallii medius*, (4) position of the stellate ganglion, (5) separate suboesophageal ganglion, and (6) homodont and " egopsid " radulae.

(5) The Cirromorpha are not, as Dollo tried to prove, highly evolved Heteroglossa, but a group of entirely distinct origin, which in many details has come to resemble the deep-water Heteroglossa (*Bathypolypus*, etc.) by convergence.

(6) The Argonautida and Heteroglossa are distinct branches of the " Incirrate " stem. The resemblance between *Tremoctopus* and the Heteroglossa seems to be mainly due to convergence (p. 47).

(7) The Bolitaenidae and Vitreledonellidae are not to be regarded as members of the same tribe. The former are to be treated as a distinct group of the same status as the Argonautida and Heteroglossa, the latter as highly modified Heteroglossa (p. 48).

(8) The Octopodidae are probably in a very active evolutionary state and only two main groups are at all clearly distinguishable. The Bathypolypodinae are characterized by their deep-water habitat and certain special features, most of which are found in the Cirromorpha. The question whether some of these characters may not be archaic is discussed (p. 49).

(9) The " Eledoninae " are not a natural group, but contain three or four very divergent genera, of which the highly modified *Thaumeledone* and *Bentheledone* are to be placed in the Bathypolypodinae.

## V. GEOGRAPHICAL DISTRIBUTION.

This order of Cephalopods has a practically universal distribution. Representatives of the three suborders of living forms occur in most of the parts of the great oceans that have been explored, though no Vampyromorpha have as yet been obtained from high latitudes. Some of the groups of Cirromorpha and Incirrata have a more localized distribution, which may cast some light on their origin and interrelationships. It is as well to remember, however, that some of these groups are as yet known from only a few species or even from single individuals. As our knowledge of the deep-sea fauna of which they are members is by no means perfect, groups which now seem to have a restricted occurrence, may ultimately be shown to be more widely distributed.

Among the Cirromorpha, *Cirroteuthis* appears to be restricted to the North Atlantic and is found within the Arctic Circle. The Opisthoteuthidae may be actually more continuously distributed than they seem to be, but at present *Opisthoteuthis* has only been recorded from the North Atlantic, and Berry's *Teuthidiscus* is the predominating Indo-Pacific genus. Very few Cirromorpha have been so far obtained from Australian and certain adjacent waters.

Of the Incirrata the Argonautida are found mainly in temperate and warm seas. Some of the groups of Heteroglossa seem to be definitely localized. The distribution of the "Eledonine" forms is discussed at length in another place (p. 51). The majority of species of *Benthoctopus* are restricted to the Atlantic, though six out of the fourteen species recognized in this work occur outside that area. The smaller genus *Bathypolypus* has five species in the Atlantic and one in Japanese waters. The four species of *Vitreledonella* are found only in the Atlantic and the sparse representatives of the small genera *Bentheledone* and *Thaumeledone* have been obtained in the S. Atlantic and Southern Ocean. The Atlantic thus seems to have been the chief scene of Octopodid evolution; but of this we cannot be sure until other areas have been more fully explored.

## VI. MEASUREMENTS AND ABBREVIATIONS.

### (*a*) *Measurements.*

The method of taking the measurements given in the text and in the various tables is the same as that explained in Vol. I (p. 38). I have not included in the main table (p. 72) any measurements of the Vampyromorpha, Cirromorpha, Ctenoglossa and Vitreledonellidae. In those groups I suspect that such measurements are valueless owing to the softness and flabbiness of the tissues. When they are used in the text they are given subject to this qualification.

### (*b*) *Abbreviations for Names of Institutions, etc.*

| | |
|---|---|
| Brit. Mus. | = British Museum (Natural History). |
| M.C. | = Cuming Collection (British Museum). |
| R.S.M. | = Royal Scottish Museum, Edinburgh. |
| Ind. Mus. | = Indian Museum, Calcutta. |
| M.H.N., Paris | = Musée d'Histoire Naturelle, Paris. |
| M.O., Monaco | = Musée Océanographique, Monaco. |
| Z.M., Berlin | = Zoologisches Museum, Berlin. |
| U.S.N.M. | = United States National Museum. |

## VII. SYNOPSIS OF CLASSIFICATION.

Order OCTOPODA, Leach.

Suborder I. *VAMPYROMORPHA*, Robson.

Fam. VAMPYROTEUTHIDAE, Thiele.

Subfam. 1. VAMPYROTEUTHINAE, Grimpe.

1. *Vampyroteuthis*, Chun.
   „ *infernalis*, Chun.
2. *Melanoteuthis*, Joubin.
   „ *lucens*, Joubin.
   „ *beebei*, Robson.
   „ *schmidti*, Joubin.
3. *Danateuthis*, Joubin.
   „ *schmidti*, Joubin.
4. *Retroteuthis*, Joubin.
   „ *pacifica*, Joubin.
5. *Hansenoteuthis*, Joubin.
   „ *lucens*, Joubin.
6. *Watasella*, Sasaki.
   „ *nigra*, Sasaki.
7. (?) *Hymenoteuthis*, Thiele.
   „ *macrope* (Berry).

Subfam. 2. LAETMOTEUTHINAE, Grimpe.

8. *Laetmoteuthis*, Berry.
   „ *lugubris*, Berry.

Suborder II. †*PALAEOCTOPODA*, Naef.

Fam. †PALAEOCTOPODIDAE, Dollo.

9. †*Palaeoctopus*, Woodward.
   „ *newboldi*, Woodward.

Suborder III. *CIRROMORPHA*, Robson.

Fam. 1. CIRROTEUTHIDAE, Keferstein.

10. *Cirroteuthis*, Eschricht.
    „ *mülleri*, Eschricht.
    (see p. 68).

Fam. 2. STAUROTEUTHIDAE, fam. n.

11. *Stauroteuthis*, Verrill.
    „ *syrtensis*, Verrill.
12. *Grimpoteuthis*, gen. n.
    „ *megaptera*, Verrill.
    „ *umbellata*, Fischer.

12. *Grimpoteuthis pacifica*, Hoyle.
,, *meangensis*, Hoyle.
,, *caudani*, Joubin.
,, *plena*, Verrill.
,, *hippocrepium*, Hoyle.
,, *mawsoni*, Berry.
,, *grimaldii*, Joubin.
,, *wülkeri*, Grimpe.
,, *glacialis*, Robson.
,, *albatrossi*, Berry.
,, sp. Hoyle, '86.
,, sp. ,, '04.
,, sp. ,, '05.
,, sp. ,, '12.
,, spp. A. and B. Robson, '24.
,, sp. Berry, 1912.
13. *Chunioteuthis*, Grimpe.
,, *ebersbachii*, Grimpe.
,, *gilchristi*, Robson.
14. *Froekenia*, Hoyle.
,, *clara*, Hoyle.
15. *Cirrothauma*, Chun.
,, *murrayi*, Chun.

Position uncertain ( ? in *Cirroteuthis*).

16. *Cirroteuthopsis*, Grimpe.
,, *massyae*, Grimpe.
(?) *Cirroteuthis hoylei*, sp. n.
,, *magna*, Hoyle.

Fam. 3. OPISTHOTEUTHIDAE, Verrill.

17. *Opisthoteuthis*, Verrill.
,, *agassizii*, Verrill.
18. *Teuthidiscus*, Berry.
,, *depressa*, Ijima & Ikeda.
,, *pluto*, Berry.
,, *persephone*, Berry.
,, *medusoides*, Thiele.
,, *extensa*, Thiele.

Suborder IV. *INCIRRATA*, Grimpe.

Tribe 1. ARGONAUTIDA, trib. nov.

Fam. 1. ARGONAUTIDAE, Tryon.

19. *Argonauta*, Linn.
,, *argo*, Linn.
,, *hians*, Solander.
,, *böttgeri*, Maltzan.
(?) ,, *cornuta*, Conrad.
,, *nouryi*, Lorois.
,, *nodosa*, Solander.
,, spp.

Fam. 2. Ocythoidae, Gray.

20. *Ocythoë*, Rafinesque.
,, *tuberculata*, Rafinesque.

Fam. 3. Tremoctopodidae, Tryon.

21. *Tremoctopus*, delle Chiaje.
,, *violaceus*, delle Chiaje.
,, *microstoma*, (Reynaud).
,, *gracilis*, (E. and S.).
,, *dubius*, (E. and S.).
,, ? *hirondellei*, Joubin.
,, ? *scalenus*, Hoyle.
,, ? *ocellatus*, Brock.
,, sp. ("*hyalinus*," Chun).

Fam. 4. Alloposidae, Verrill.

22. *Alloposus*, Verrill.
,, *mollis*, Verrill.
,, *hardyi*, Robson.
,, *pacificus*, Ijima.
,, sp. Joubin.
23. *Alloposina*, Grimpe.
,, *albatrossi*, n.n.

Tribe 2. HETEROGLOSSA, Naef.

Fam. 1. Octopodidae, Orbigny.

Sub-fam. Octopodinae, Grimpe.

24. *Octopus* Lamarck. (See Part I.)
Subgenus 1. *Octopus*, Lamarck.
2. *Macrotritopus*, Grimpe.
3. *Tritaxeopus*, Owen.
4. *Macroctopus*, Robson.
5. *Enteroctopus*, Rochebrune & Mabille
25. *Cistopus*, Gray. (See Part I.)
26. (?) *Pinnoctopus*, Orbigny. ,,
27. *Joubinia*, Robson. ,,
28. *Scaeurgus*, Troschel. ,,
29. *Paroctopus*, Naef. ,,
30. *Macrochlaena*, Robson. ,,
31. *Pteroctopus*, Fischer. ,,
32. *Hapalochlaena*, Robson. ,,
33. *Benthoctopus*, Grimpe.
,, *piscatorum*, (Verrill).
,, *levis* (Hoyle).
,, *eureka*, (Robson).
,, *berryi*, Robson.
,, *sibiricus*, Løyning.
,, *lothei* (?) (Chun).
,, *hokkaidensis*, (Berry).
,, *thielei*, sp. n.

33. *Benthoctopus januarii*, (Hoyle).
,, *profundorum*, sp. n.
,, *abruptus*, (Sasaki).
,, *magellanicus*, Robson.
,, *ergasticus* (P. & H. Fischer).
,, *pseudonymus*, Grimpe.
34. *Teretoctopus*, Robson.
,, *indicus*, Robson.
,, *alcocki*, sp. n.
35. *Grimpella*, Robson.
,, *thaumastocheir*, Robson.
36. (?) *Haptochlaena*, Grimpe.
,, *chuni*, Grimpe.
37. *Eledone*, Leach.
,, *moschata* (Lamarck).
,, *cirrosa* (Lamarck).
38. *Pareledone*, new genus.
,, *charcoti*, Joubin.
,, *turqueti*, Joubin.
,, *polymorpha*, Robson.
,, *harrissoni*, Berry.
,, *adelieana*, Berry.
,, *nigra*, Hoyle.
,, *antarctica*, Thiele.
,, sp. ("*brevis*," Massy, '16).
39. (?) *Eledonenta*, Rochebrune.
,, *microsicya*,
,, *filholiana*.
40. *Velodona*, Chun.
,, *togata*, Chun.

Subfam. 2. BATHYPOLYPODINAE, Robson.

41. *Bathypolypus*, Grimpe.
,, *arcticus*, Prosch.
,, *lentus*, Verrill.
,, *obesus*, Verrill.
,, *sponsalis*, Fischer.
,, *salebrosus*, Sasaki.
,, *valdiviae*, Thiele.
42. *Graneledone*, Joubin.
,, *challengeri* (Berry)
,, *verrucosa*, Verrill.
,, *setebos*, sp. n.
43. *Thaumeledone*, Robson.
,, *brevis*, Hoyle.
,, *gunteri*, Robson.
44. *Bentheledone*, gen. n.
,, *rotunda*, Hoyle.
,, *albida*, Berry.
,, spp. ("*rotunda*," "*verrucosa*," Hoyle, '04).

Fam. 2. VITRELEDONELLIDAE, Robson.

45. *Vitreledonella*, Joubin.

45. *Vitreledonella*, *richardi*, Joubin.
„ *alberti*, Joubin.
„ *ingeborgae*, Joubin.
„ *translucida*, Robson.

Tribe 3. CTENOGLOSSA, Naef.

Fam. 1. Bolitaenidae, Naef.

46. *Bolitaena*, Steenstrup.
„ *microcotyla*, Hoyle.
„ *massyae* (Robson).
„ *ijimai* (Sasaki).
47. *Eledonella*, Verrill.
„ *pygmaea*, Verrill.
48. *Iapetella*, Hoyle.
„ *prismatica*, Hoyle.
„ *diaphana*, Hoyle.
„ *heathi* (Berry).

Fam. 2. Amphitretidae, Hoyle.

49. *Amphitretus*, Hoyle.
„ *pelagicus*, Hoyle.
„ *thielei*, Robson.

*Incertae Sedis.*

50. *Heptapus*, Joubin.
„ *danai*, Joubin.

# VIII.—TABLE OF MEASUREMENTS.

For explanation of the measurements and indices see Vol. I ("Variation" and p. 38). The Vampyromorpha, Cirromorpha, Ctenoglossa and Vitreledonellidae are not included in these tables (p. 66).

| ARGONAUTIDAE. | Total length (mm.). | Eye-apex (mm.). | Width index. | Interocular index. | Arms, formula, or measurements. | Arms, index. | Suckers, index. | Web, formula or length of sectors. | Web, index. |
|---|---|---|---|---|---|---|---|---|---|
| *Ocythoë tuberculata* (♀). | | | | | | | | | |
| Brit. Mus. | 475 | 140 | 64 | 42 | 4.1.2=3 | 70 | 3·5 | A.B.C.D.E.(?) | — |
| Sasaki (1929) | 470 | 140 estim. | 72 | 50 | 4.1.2.3 | 61 | 4·5 | — | — |
| | 345 | 100 ,, | 75 | 55 | 1.2.3.4 | ? | — | — | — |
| | 520 | 185 ,, | 75 | 43 | 1.4.2.3 | 66 | 4·3 | — | — |
| | | | | | 1=4, 2.3 | | | | |
| Jatta (1896) | 370 | — | — | — | 1=4, 2=3 | 70 | — | — | — |
| Vérany (1851) | 840 | — | — | — | 1=4.2.3 | 61 | — | — | — |
| *Tremoctopus violaceus* (♀). | | | | | | | | | |
| Brit. Mus. | 268 | 65 | 73 | 61 | 2.1=4.3 | 75 | 5·3 | 70 106 32 29 11 | 52 |
| Sasaki (1929) | 470 | 120 | 154(?) | 75 | — | 68 | 5·0 | 120 200 80 50 40 | 62 |
| | 440 | 90 | 100 | 100 | — | 75 | 5·8 | — 140 65 50 70 | 42 |
| | 300 | 76 | 53 | 60 | 1.2.4.3 | ? | 4·6 | 50 100 35 30 20 | ? |
| Neviani (1927) | 289 | 112+ | 72± (fig.) | 72± | 2.1.4.3 | 61 | — | — | — |
| Jatta (1896) | 210 | 60 | 53 (fig.) | — | 2.1.4.3 | 85 | — | — | — |
| Berry (1914) | 64+ | 22 (calc.) | 68 | 70 | 40+.33+.20.32 | 69 | — | 14.22 — — 3 | 48 |
| | | | | | 40+.45.20.32 | | | | |
| | 51+ | 15 calc. | 73 | 80 | 37+.37.15.25 | 72 | — | 13.17 — — 3 | 45 |
| | | | | | 27+.34+.15.25 | | | | |
| Degner (1925) | — | 7 | — | — | 8.5.3.4 | 53 | — | — | — |
| | — | 7 | — | — | 8.6.3.4 | 53 | — | — | — |
| | — | 7 | — | — | 8.5·5.2·5.4 | 53 | — | — | — |
| Joubin (1929) | 51 (incl. hectocotylus) 32 = arms + mantle | 13 | 84 | 84 | 18 19 10 14 | 59 | — | — | ⅔ of dorsal arms. |
| Naef (1923) (fig.) | — | 28 | 60 | 75 | 110.68.38.27 | 79 | — | 38.41 — — — | 37 |
| *violaceus* (♂). | | | | | | | | | |
| Jatta (1896) | 35 | 15 | ? 96 (fig.) | 92 (fig.) | 20.25.10.15 | 71 | — | — | — |
| | | | | | 40 × | | | | |
| Naef (1923) (fig.) | c. 35 | 15 | c. 73 | c. 76 | 20.19 ?10.13 | 57 | — | 99 ?4·5 ?4·5 ?4·5 ? | 45 |
| Berry (1914) | 30 | 10 | 70 | 80 | — | 60 | — | 6 6 — — 1 | 33 |
| | 25 | 7·5 | 93 | 100 | — | 64 | — | 3·5 3·5 — — 1 | 21 |
| | 24+ | 8 | 120 | 112 | — | — | — | 6 5 — — 3 | 42(?) |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Argonauta* | | | | | | | | | |
| *argo* (♀). | | | | | | | | | |
| Brit. Mus. | c. 300 | 70 | 60 | 47 | — 230 140 230(?) | 76 | 5·9 | — | — |
| Jatta | 150 | 50(?) | — | — | 85 95 80 105 | ?70 | — | — | — |
| Vérany | 330 | 100(?) | — | — | (260) 190 170 210 | 78 | — | — | — |
| Orbigny | 280 | 60(?) | — | — | 125 170 130 200 | 71 | — | — | — |
| *böttgeri* (♀). | | | | | | | | | |
| Massy "T. Nova" | — | 10 | 80 | 90 | 8 11 10 ?11 ? 8 12 — 9 | 59 | 10 | | |
| Berry | — | 22? | 59 | 59 | | — | 9·0 | | |
| (The figures given by Sasaki (1929) are not of sufficient value to utilize here. | | | | | | | | | |
| *hians*. | | | | | | | | | |
| Orbigny (juv.) | 55 | 12 | 116 (see text) | | 17 30 28 28 | 54 | | | |
| ,, (adult)? | ? | | ? | ? | ? 60 50 40 | | | | |
| Sasaki | 56–12 | | <100 | | 1.2.3.4 | 66 (calc.) | | | |
| *nodosa* ("*tuberculata*"). | | | | | | | | | |
| Orbigny | 216 | 66 | 53 | | 130.135.118.125 | 62 | | | |
| *Alloposus* | | | | | | | | | |
| *mollis*. | | | | | | | | | |
| Verrill 1880*b* | 160 | 75–70 | 100 | | — | 43 | — | — | — |
| ,, 1882 | — | | 100(?) | | ?1.2.3.4 | — | — | ABCDE | 59 (fig.) |
| ,, 1882, p. 420 | 812 | — | — | | 2.1.3=4 | 72 (calc.) | — | — | — |
| Joubin 1895 | 670+ | — | — | | 1.2.3.4 | — | — | A.B.C=D.E | 26 |
| ,, 1900 | 1610+ | — | — | | 1.2.3.4 | | | A.E.D.C.B | 37 |
| (?) Berry (1914) | 147+ | 50? | 92 | | 2.1.3.4? ?2.1.4.3 | 61 | 8 | 54 — — — 44 | 60 |
| *pacificus*. | | | | | | | | | |
| Sasaki (1929) | 120 | 30? | 133 | | 1.2.3.4 | 79 | — | A.B.C=D=E | 57 |
| *hardyi*. | | | | | | | | | |
| Type | 152 | 40 | 87 | | ?1.2.3.4 | 73 | — | A.B.C.D.E | c. 33 |
| *Alloposina*. | | | | | | | | | |
| *albatrossi* | | | | | | | | | |
| Hoyle (1904) | 18 | 10 | 150 | | 1.2.3=4 | ? (see text) | 10 | — | — |

## Table of Measurements—(*continued*).

| | 1. Dorsal length of mantle (mm.). | 2. Width index. | 3. Inter-ocular index. | 4. Arms, formula. | 5. Arms, length. | 6. Suckers, index. | 7. Web, formula. | 8. Web, depth (index). | 9. Hectoco-tylus (index). | 10. Sculpture. | 11. Colour. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| OCTOPODIDAE. | | | | | | | | | | | |
| OCTOPODINAE. | | | | | | | | | | | |
| *Benthoctopus.* | | | | | | | | | | | |
| 1. *piscatorum* Verrill | | | | | | | | | | | |
| ♀(♂ ligula only) | 39 | 79 | 76 | 2.1.3.4 | 75 | 6·4 | A=B=C=D.E. | 25 ?+ | — | Smooth | Deep purplish brown; eye-lids whitish; base of funnel. |
| Brit. Mus., ♀ | 51 | 100 | 68 | 3.1.2=4 | 75 | 8–7 | B=C.A.D.E | 31 | — | ,, | Light purplish brown. |
| Massy, ♂ | 42 | 71 | 76 | 1.2.3.4 | 76 | 9·5 | A>rest<br>E<rest | 25+ | 5–4 | ,, | Warm vinous, patches of bluish grey on web between arms on ventral side. |
| Russell, ♂♀ | 32–19 | "globular" (?100) | 88–63 | 4.1=2.3<br>2.1.4.3<br>4.1.2.3<br>etc. | 81–79 | 7(♂)<br>9(♀) | — | — | 6·5 | ,, | Deep purplish red. |
| 2. *levis* | | | | | | | | | | | |
| type ♂ | 50 | 80 | 70 | 4.2.1.3<br>1=2.3=4 | 73 | 6 | | 35 | 7·0 | ,, | Dull grey. |
| ,, ♂ (?) Indian Museum | 47 | 89 | 76 | — | 75 | 8 | C.B.A=D.E | 34 | 9·0 | ,, | — |
| (Massy), ♀ | 30 | 66 | 56 | 2.1.3.4<br>2.1.4.3 | 67 | 6 | — | 33 | — | ,, | Slate blue (see text). |
| ♀ | 27 | 81 | 66 | 4=3=2.1 | 68 | 6 | C=D.E.B.A<br>(? C=D, E=B=A) | 43 | — | ,, | — |
| 3. *eureka* type | (See Vol. I, p. 52) | | | | | | | | | | |
| 4. *berryi* type ♀ | 47(?) | 93 | 93 | ?1=2.3.4 | 72 | 3·2 | C.A=B=D.E | 26 | — | ,, | Light purplish brown (see text). |
| 5. *sibiricus* type ♂ | (See text) | | | | | | | | | | |
| 6. *lothei* Chun (1914), ♀ | 80 | 87 | 87 | 1.2.3.4 | 81 ? | 6·2 | — | 33 | — | ,, | Light greyish violet. |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 7. *hokkaidensis* | | | | | | | | | | | |
| Sasaki, 1929, ♂♀ | 58–35 | 102–88 | 94–82 | ? 1.2.3=4 | 70–66 | 8·6–6·8 | (?) A=B=C=D.E | 27–24 | 4·6 | ,, | — |
| U.S.N.M., 332980 | 40 | 87 | 82 | 1.2=3=4 | 79 | 7·4 | A.B=C=D=E | 28 | — | ,, | Purplish brown (see text). |
| 8. *thielei* (see remarks, p. 235) | | | | | | | | | | | |
| type ♂ | 65 | 93 | 80 | 1=2=3=4(?) | 73 | 9 | ? C=D.B=E.A | 25 | 13 | ,, | See text. |
| 9. *januarii* | | | | | | | | | | | |
| type ♂ | 47 | 97 | 68 | ? 1.2.3=4 | 87 | 7·4 | A.C.B.D.E | 23 | ?6·9 | ,, | Pale purplish pink, paler below. |
| 10. *profundorum* | | | | | | | | | | | |
| type ♂ | 47 | 85 | 69 | ? 1.2.4.3 | 83 | 5·9 | C.A=B=D.E | 34 | 6·9 | ,, | — |
| Sasaki, ♀ (see p. 238) | 67–52 | 78–71 | 86–70 | 1.2.3.4 | 78–71 | 6·7–5·9 | C.A=B=D.E A.B.C=D.E etc. | 26–24 | — | ,, | "Purplish pink to a darker shade deepening to black on the aboral surface of the arms." |
| 11. *abruptus* | | | | | | | | | | | |
| Sasaki, 1929, ♂ | 98 | 66 | — | 1.2.4.3(?) | 78 | 15 | A=B=C=D.E | 24 | 7·6 | ,, | — |
| Paratype ♀ | 63 | 100 | 84 | 2.3.1.4 | 82 | 8 | A.D.C=B.E | 23 | — | — | ? Purplish brown. |
| 12. *magellanicus* | — | c. 100 | 83–78 | 2.3.1=4 | 78–74 | 13–9·2 | C.B=A.D.E B.A.C.D.E | 32–31 | 8·5 | See text | (?) Light purple with irregular dark blotches. |
| 13. *ergasticus* | | | | | | | | | | | |
| type ♂ | 45(?) | 88 | 73 | 1.2.3.4 | 84 | 4·9 | A.B.C.D.E | 27 | 7·0 | Smooth | Vinous red. |
| Massy, 1909, ♂♀ | 111–60 | 93–63 | 89–55 | 1.2.3.4 | 87–77 | 8–3·3 | — | 28–20 | (?) 13–7·5 | ,, tuberculate around eyes | Vinous. |
| 14. *pseudonymus* | | | | | | | | | | | |
| Joubin (♀ ?) | 40 | 109 (fig.) | 104 (fig.) | 1=2=3=4 | 69(?) | — | — | ?33 | — | Smooth | Violet. |
| *Teretoctopus* | | | | | | | | | | | |
| *indicus*, ♂ type | 31–24 | 60–48 | 40–37 | — | 71–69 | 4·4–3·5 | A=B=C=D.E | 40–35 | 6·3–5·5 | ,, | — |
| *alcocki* type ♂♀ | 60–27 | 63–55 | 51–46 | ? | 79–72 | 6·6–5·0 | ? | 34–29 | 16–12 | ,, | — |
| *Grimpella* | | | | | | | | | | | |
| *thaumastocheir* type ♂ | 25 | 100 | 88 | 2=3=4.1 | 82 | 22 | ? A=B=C=D=E | 30 | 10 | Large and small warts usually simple | ? Originally purplish brown. |
| *Haptochlaena* | | | | | | | | | | | |
| *chuni* | (See text, p. 256) | | | | | | | | | | |

## TABLE OF MEASUREMENTS—(*continued*).

| | 1. Dorsal length of mantle (mm.). | 2. Width index. | 3. Inter-ocular index. | 4. Arms, formula. | 5. Arms, length. | 6. Suckers, index. | 7. Web, formula. | 8. Web, depth (index). | 9. Hectoco-tylus (index). | 10. Sculpture. | 11. Colour. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eledone* | | | | | | | | | | | |
| 1. *moschata* | | | | | | | | | | | |
| Brit. Mus. ♂♀ | 53–62–80 | 55–69–82 | 40–49–57 | 2.1.3.4<br>2.3.1.4<br>etc. | 73–76–81 | 11–22 | A.B.C.D.E<br>etc. | 29–30–34 | 2·8 | Smooth | "Greyish brown with blackish brown blotches (Naef)." |
| 2. *cirrosa* | | | | | | | | | | | |
| Brit. Mus. ♀♂ | 57–71–110 | 40–73–109 | 41–52–75 | ? | 67–73–81 | 9–13 | ? A=B=C.D.E | 21–29–41 | 2·7–3·7 | Granular | "Yellowish brown with rust-brown blotches" (*id.*). |
| *Pareledone* | | | | | | | | | | | |
| 1. *charcoti* | | | | | | | | | | | |
| Joubin (type) | 34 calc. | 105 | 73 | 3.1.4.2 | 62 | — | | "$\frac{1}{2}$–$\frac{1}{3}$" | — | See text | — |
| Exp. Franç. 2me. (G.C.R.) | 24–22 | 104–100 | 79–86 | Subequal | 66 (1 only) | — | C.D=B.A.E | 39–31 | — | ,, | — |
| "Terra Nova" St. 294. B.M. | 39–26 | 100–96 | 75–73 | ,, | 72–65 | 9–6·4 | A=B=C=D.E (one only) | 41–23(?) | 7·7 | ,, | — |
| Massy (6) "Terra Nova" Stns. 349, 338 | 50–53 calc. | 127–86 | 100–53 | 2=413<br>4123, etc. | 72–60 | 11·1–4·6 | — | — | 8·1–5·6 | ,, | ? |
| Berry (1917) as "*aurorae*" | 24 | 104 | 87 | 2=413<br>4=321 | 62 | — | "of nearly equal extent all around"<br>E>rest | 33–25 | 4·6 | ,, | Dark slaty grey above, clouded with dim mottlings, very pale ventrally. |
| "Discovery," 1930 | 74–28 | 116–93 | 84–60 | Subequal | 72–62 | 12–8·3 | A=B=C=D.E<br>or<br>C=D, B.A=E | 42–22 | 11–8 | ,, | See text. |
| 2. *turqueti* | | | | | | | | | | | |
| Joubin (1906) | 14(?) | 100(?) | 100(?) | ,, | 66 | — | A>rest<br>E ? absent | 20 | — | ? Very finely granular | ,, |
| ,, (1914) | 18 | 125 (fig.) | 113 (fig.) | — | — | — | | 50+ (fig.) | — | Rudimentary tubercles | Violet. |
| Massy (1916) (remeasured) | 56–40 | 108–71 | 83–61 | — | 72–64 | 9·8–7·4 | — | 38–28 | 7·8 | Smooth or (?) granular | — |
| "Discovery," 1930 | 43–37 | 93–94 | 86 | | 72–64 | 11·5–7·4 | — | 25–20 | 7–6 | ,, ,, | Light reddish purple. |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 3. *polymorpha* form *oblonga*, ♂ "Discovery," 1930 | 50–41 | 75–64 | 69–61 | Subequal | 72–65 | 8–7 | D.B=C, A=E | 40–35 | 15–13·9 | Finely granular | Pale purplish brown to fawn. |
| form *affinis*, ♂ "Discovery," 1930 | 66–30 | 104–70 | 93–53 | ,, | 71–66 | 10–7 | ? Subequal E<A | 30–27 | 17–9 | ,, | Greyish purple or slate grey. |
| 4. *harrissoni* Berry (1917) | 51–39 | 140–115 | 100–88 | 2=3=4.1(?) | 70–65 | 8·8(?) | "bilateral" ? E>A | 25 | — | "A number of low conical papillae on dorsum and sides" | Dull clouded slaty grey. |
| 5. *adelicana* (*id.*) | 38 ("dorsal") | 100 | 86 | ? Subequal | 69 | 7·8 | ? | 25— | | Smooth | As 4, only slightly paler below: a subperipheral pale line. |
| 6. *nigra* Hoyle | 40 | 80 | 55 | "Subequal" | 78 | 15 | E<A | 25(?) | — | Smooth (? trace of "shagreen") | "Almost black." |
| 7. *antarctica* Thiele | 115–95 (See text) | 52–63 | 57–52 | 4>1 | 65–62 | 5·2–6·3 | E>A | 32–16 | (?)4·2 | Smooth or warty | Grey-yellow. |
| 8. sp. (= "brevis," Massy, 1916) | (See text, p. 281) | | | | | | | | | | |
| *Eledonenta* | (See text, p. 281) | | | | | | | | | | |
| *Velodona ogata* Chun | 111 | 79 | 73 | 1.2.3.4 | ? | — | See text | — | — | Fine warts | Very pale ground-colour lightly blotched dorsally with light brown (fig.). |
| var. *capensis* Kolbson | 60–38 | = type | = type | 1.2.3.4 | 78–77 | — | CB=ADE | — | See text | = type | Deep reddish brown. |

TABLE OF MEASUREMENTS—(*continued*).

| | 1. Dorsal length of mantle (mm.). | 2. Width index. | 3. Inter-ocular index. | 4. Arms, formula. | 5. Arms, length. | 6. Suckers, index. | 7. Web, formula. | 8. Web, depth (index). | 9. Hectoco-tylus (index). | 10. Sculpture. | 11. Colour. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Bathypolypodinae. | | | | | | | | | | | |
| *Bathypolypus arcticus* | | | | | | | | | | | |
| Brit. Mus., ♂♀ and Leiden Museum, ♂ | 34–56 | 82–94–102 | 73–81–100 | 1.2.3.4<br>1.2.3=4<br>etc. | 69–72–76 | 2·0–4·7–7·0 | A.B.C.D.E<br>A=B.C.D.E<br>etc. | 38–32–25 | 38–30–17 | i. Irregular, simple or multifid warts (sparse or numerous)<br>ii. Stellate warts<br>iii. i and ii. ocular cirri | Light purple, uniform or maculate. |
| Zool. Mus., Berlin, ♀ | 66–43 | 97–63 | 58–45 | 1=2.3.4<br>1.2.3.4 | 72–67 | 7·4–5·7 | A.B.C=D.E<br>A.B=C=D.E | 44–41 | — | Stellate warts | Light purple. |
| Verrill, 1882 ♂ only | 53–44 | (?)90–70 | 77–40 | 3.2.1=4 | c. 70 | — | — | c. 33 (from fig.) | 38 | Conical, irregular and often rough tubercles. Prominent ocular cirri; minute scattered papillae | Pale bluish white, thickly speckled with light and dark chromatophores. |
| "Challenger," Brit. Mus. | 35–31 | 100–90 | 69–64 | 1.2.3.4<br>etc. | 75–72 | — | ? A=B=C=D.E | 36–30 | 10 | Stellate papillae | (Discoloured). |
| "faeroensis" (Russell) | 48–40 | 85–75 | 62–59 | 1.2.3.4 | 78–77 | — | — | 28–24 | 12–11 | ,, | Fine reddish purple. |
| "faeroensis," Scottish Fishery Board, ♂ and ♀ | 46–17 | 88–61 | 76–54 | 1.2.3.4<br>etc. | 72–67 | 7·6–5·9 | A.B.C.D.E<br>A.B=C.D.E | 46–33 | 12 | ,, | ,, ,, |
| *lentus* | | | | | | | | | | | |
| Verrill, ♀ | 60 | 66 (text), 78 (fig.) | 53 (text) | 1=3.2.4<br>1=3, 2=4 | 57 | — | B.A=C.D.E | — | | Small ocular cirri (? Body sculpture absent). | Deep reddish brown, many round whitish spots. |
| ♂ | 34 | 82 | 64 | ? 1.2.3.4 | 68 | — | — | (?) 33 | 39 | As above with a small number of minute white papillae | — |
| Grieg | 42 | 100 | — | — | 64 | — | — | 32 | — | — | See text. |
| Nordgård | 40 (?) | — | — | — | ?69 | — | — | — | — | — | — |
| *obesus* | | | | | | | | | | | |
| Verrill, ♂ | 72 | 63 | 52 | 1.2.4.3<br>? 1=2.3.4 | 66 | 4·1 | — | ?27 | 34 | Smooth: no cirri (?) | Pale pinkish, speckled with reddish-brown spots (?). |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *sponsalis* Type, etc., ♂♀ (M.N.H., Paris) | 35–39 | 100–75(?) | 90–70 | ? 1.2.4.3 | 77–68 | 5·5–3·4 | ? A=B=C=D.E B.C=A=D.E | 33–25 | 17–16 | ? Sometimes smooth. More often a mass of blister-like pustules round eyes and more sparsely on dorsum and head | Uniform deep purple. |
| *valdiviae* type, etc., ♂♀ | 34–27 | 79–72(?) | 83–76 | ? 1=2=3=4 | 71–68 | 6·5–5·9 | ? A=B=C=D.E | 40–34 | 15 | Flat subgranular warts well developed about eyes, one ocular cirrus | Reddish brown. |
| *"grimpei"* Brit. Mus., ♂♀ | 40–22 | 105–86 | 90–80 | ?1=2=3=4 | 72–66 | 5–4·3 | ? A=B=C=D.E | 40–33 | 18 | = above no cirri | ,, |
| S. African Museum, ♂ | 33–27 | 100–77 | 84–77 | ? 1=2.4.3 | 74–71 | 5·5–3·9 | A=B=C.D.E A=B, C=D.E | 41–37 | 13 | As above cirri present | ,, |
| *salebrosus* Sasaki, ♀ | 45–23 | 105–91 | 91–84 | ? 1=2=3=4 | 65–58 (?) | 9·3–7·8 | A=B=C=D.E | 33–28 | — | Thickly beset with coarse roundish warts tending to become linear on sides and ventral surface | "Light cardinal to claret." |
| *Graneledone challengeri* (type) | 74 | ?90 | 80 | ? 2.1.3.4 | 76 | 7·0 | ? A=B=C=D.E | 30 | 3·3 | Small multifid papillae (see text) | Dull brownish purple. |
| *verrucosa* Verrill, 1881, 1884 | 100–58 | 96–65 | 92–84 | 1.3.2.4 2.1.3.4 etc. | 85–72 | 6·4–5·0 | — | ? 39–25 | 7·0–3·4 | See text | "Dark purplish brown, darker purple beneath." |
| Yale Univ., "Albatross," Stn. 2077 | 25 | 100 | 97 | Subequal | 72 | 6 | ? C=D=B.A.E | 39 | — | ,, | Uniform medium purple. |
| *media* (type) ♂ | c. 86 | 121 (?) | 120 | See text | 76 | — | D.E.C.B.A | 37 | 4·9 | Small multifid papillae | Greyish violet dorsally; reddish-grey violet ventrally. |
| *setebos* (type) B.M. | (See text) | | | | | | | | | | |

TABLE OF MEASUREMENTS—(*continued*).

| | 1. Dorsal length of mantle (mm.). | 2. Width index. | 3. Inter-ocular index. | 4. Arms, formula. | 5. Arms, length. | 6. Suckers, index. | 7. Web, formula. | 8. Web, depth (index). | 9. Hectoco-tylus (index). | 10. Sculpture. | 11. Colour. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Thaumeledone* | | | | | | | | | | | |
| 1. *brevis* (type) | 20 | 110 | 100 | Subequal | 63 | 5 | A=B=C.D.E | 68 | — | ? Finely granular ocular cirri | See text. |
| 2. *gunteri* (type) | 36 | 111 | 86 | (?) ,, | 57 | 8·3 | Subequal | 60 | — | See text | Rich light purple. |
| *Bentheledone* | | | | | | | | | | | |
| 1. *rotunda* (type) | 55 | 81 | 63 | ? 1=2=3=4 | 66 | 4·9 | A.D.B=C.E | 43 | — | Smooth | Light purple. |
| 2. *albida* Berry (1917) | 35 (dorsal) | 114 | 88 | "Roughly subequal" | 75 | ?8 from fig. | A>E | 33+ | — | ,, | Greyish white (alcohol). |

## IX. BATHYMETRICAL RECORDS.

In the following tables are given the depths from which the various species have been obtained, the gear by which they were caught, etc. From these and other data it will be possible to form an estimate as to the habitat of some of these forms (see discussion, p. 18). In cols. 4 and 5 are given (when known) the sounding at the station and the depth from which a given specimen was recorded as obtained. More often than not these depths are identical. When a trawl is used and bottom fauna is collected, the depth from which a specimen was obtained is usually entered by authors as that of the actual sounding, irrespective of whether the specimen may have entered the trawl on the bottom or more or less off it (see p. 19). In the case of forms suspected of living off the bottom which have been caught in nets, it is important to distinguish " sounding " from the depth to which the net was lowered. When a depth is given without any specification as to whether it was the bottom sounded or that to which a net was lowered, I have refrained from attempting to estimate the bottom-depth from the map as the probability of error is usually too large, especially in depths down to 1000 fathoms.

Very special stress must be laid on the necessity of checking the data of individual authors. The existence of two sets of data (soundings and depth at which specimens are obtained) introduces a possibility of error, as (*e.g.*) when soundings are given for the depth of catch. Thus Sasaki (1920, p. 167) gives 500 fathoms as the depth at which *Argonauta hians* was taken. Reference to the official " Albatross " Report shows that the catching was done at the surface!

I have noted in col. 7 certain discrepancies that seem to occur between the data given by Hoyle (1904) for the deep-water fauna of the E. Pacific explored by the " Albatross " and those given in the Station list (" Reports U.S. Fish Commission, 1894 "), *e.g.* Hoyle's Station 3366 has date February 27, 1891, that in the Report has August 9, 1893. There are also some discrepancies between the data given by Joubin (1929) and the " Dana " Station List.

| 1. | Authority. 2. | Cruise and station. 3. | Sounding (bottom depth) fms. 4. | Depth given for specimen (fms.). 5. | Gear. 6. | Remarks. 7. |
|---|---|---|---|---|---|---|
| Vampyromorpha. | | | | | | |
| *Vampyroteuthis infernalis* | Chun (1914) | "Michael Sars" 57 | | 1094 | | |
| ,, ,, | ,, ,, | ,, 51 | 2125 | 1641 | "Catcher" (?) | Larvae [sic]. |
| ,, ,, | Thiele (1915) | "Valdivia" 65 | | 656 | Vertikalnetz | "Vertikalnetz in 1200 m. herabgelassenen." |
| ,, ,, | ,, ,, | ,, 67 | | 2188 | ,, | "Vertikalnetz in 4000 m. herabgelassenen." |
| *Melanoteuthis lucens* | Joubin (1920) | "Pr. Alice" 2118 | | 1895 | Chalut à plateaux | |
| ,, ,, | ,, ,, | ,, 2168 | | 0–1094 | Filet Richard à grande ouverture | |
| ,, ,, | ,, (1929) | "Dana" 1261 | 2921 | ? | | Joubin does not give exact haul. |
| ,, *beebei* | Robson (1929) | "Arcturus" | ?=5 | 0–750 | Otter trawl | |
| ,, *schmidti* | Joubin (1929) | "Dana" 1261, ix | 2921 | 1094 | Stramin net (open) | Joubin gives 2000 m. for specimen; Station list has 3000 m. for "(9)." |
| ,, ,, | ,, ,, | ,, 1267, v | ? | 727 | ,, ,, | Joubin gives 1330 m. for specimen; Station list gives 2000 mm. for "(5)." |
| ,, ,, | ,, ,, | ,, 1358 ? | ? | 1094 | ,, ,, | |
| *Danateuthis schmidti* | ,, ,, | ,, 1217, iv | ? | 908 | Stramin net | ? Joubin's depth. |
| *Retroteuthis pacifica* | ,, ,, | ,, 1203, ix | 1394 | 1274 (Joubin) 19–0 ! (Station list as "wire out") | Nansen closing net (?) | ,, ,, ? Joubin's error or Station list's. *N.B.* Joubin's time of day does not agree with Station list 1203, 9. |
| *Hansenoteuthis lucens* | ,, ,, | ,, 1242 ? | 1969 | 583 (?) | ? | Joubin does not cite the sub-station number so that "wire out" is uncertain. |
| ,, ,, | ,, ,, | ,, 1269 ? | 2324 | 728 (?) | ? | ,, ,, ,, |
| ,, ,, | ,, ,, | ,, 1283 ? | 1159 | 911 (?) | ? | ,, ,, ,, |
| ,, ,, | ,, ,, | ,, 1322 ? | ? | 1094 (?) | ? | ,, ,, ,, |
| ,, ,, | ,, ,, | ,, ? | ? | 1274 (?) | ? | ,, ,, ,, |
| *Laetmoteuthis lugubris* | Berry (1914) | "Albatross" 3904, 3898 | 258–295 | Surface and 284 | | Fragments. |
| *Hymenoteuthis macrope* | ,, (1912) | ,, 4393 | | 2259–2113 | 8′ Tanner beam trawl | |
| *Watasella nigra* | Sasaki (1920, 1929) | ,, 4977 | 544 | 544 | 9′ Agassiz trawl | |
| Cirromorpha. | | | | | | |
| *Cirroteuthis mülleri* | Eschricht | — | ? | ? | ? | Probably in shallow water. |
| ,, ,, | Prosch and Reinhardt | | ? | ? | ? | |
| ,, ,, | Appellöf (1893) | Norwegian N. Atlantic Exp. 297 | ? | 1280 | Trawl | |
| ,, | Friele and Grieg (1901) | 2nd ditto | ? | ? | ? | (Where ?). |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Stauroteuthis syrtensis* | Verrill (1879) | Fishermen | | | 250 | | |
| ,, ,, | ,, (1885) | "Albatross" 2034 | | 1346 | 1346 | Beam trawl | |
| ,, ,, | ,, (*l.c.*) | ,, 2180 | | 523 | 523 | Large beam trawl | |
| *Cirroteuthis* (?) *magna* | Hoyle (1886) | "Challenger" 146 | | 1375 | 1375 | Trawl | |
| ,, (?) *hoylei* | Hoyle (1886) as *C. magna* | ,, 298 | | 2225 | 2225 | ,, | |
| *Grimpoteuthis meangensis* | Hoyle (1886) | ,, 214 | | 500 | 500 | ,, | |
| ,, ,, | ,, ,, | ,, 171 | | 600 | 600 | ,, | |
| ,, ,, (?) | Lo Bianco (1903) | "Puritan" 39 | | 601 | 1258 | "Slitta di fondo" | "Cavo filato." |
| ,, *pacifica* | Hoyle (*l.c.*) | "Challenger" 181 | | 2440 | 2440 | Trawl | |
| ,, *umbellata* | Fischer (1883) | "Talisman" 45, 80, 130 | | ? | 1222–623 | | |
| | Joubin and Fischer (1907) | | | | | | |
| ,, ,, | ,, | "Talisman" 130–79 *bis.* | | ? | 1222–623 | | |
| ,, ,, | Joubin (1900) | "Princesse Alice" 753 | | ? | 2388 | Chalut | "Il est possible que l'animal ait été capturé par le filet à la montée." |
| ,, ,, | ,, (1920) | ,, 2986 | | ? | 2664 | ,, | |
| ,, ,, | ,, ,, | ,, 2994 | | ? | 2735 | ,, | |
| ,, ,, | ,, (1924) | ? 3412 | | ? | 2882 | ,, | |
| ,, ,, | Chun (1914) | "Michael Sars" 53 (only) | | 1567 | 1430 | Catcher | See text. |
| ,, *megaptera* | Verrill (1885) | "Albatross" 2225 | | 2512 | 2512 | ? | Possibly large beam trawl. |
| ,, ,, | ,, ,, | ,, 2224 | | 2574 | 2574 | ? | ,, ,, ,, ,, |
| ,, ,, | ,, ,, | ,, 2220 | | 1054 | 1054 | ? | ,, ,, ,, ,, |
| ,, ,, | Joubin (1920) | "Princesse Alice" 1150 | | ? | 2128 | Chalut | |
| ,, *gilchristi* | Robson (1924) | "Pickle" 526 | | 1073 | 1400 | Reversible trawl | Mixed fauna (benthos and nekton). |
| ,, *plena* | Verrill (1885) | "Albatross" 2205 | | | 1073 | Large beam trawl | |
| ,, *caudani* | Joubin (1896) | | | | 355 | | |
| ,, *albatrossi* | Sasaki (1920, 1929) | "Albatross" 4771 | | 426 | 426 | 12′ Tanner beam trawl | |
| ,, ,, | ,, ,, | ,, 5029 | | 440 | 440 | 9′ Agassiz trawl | |
| ,, ,, | ,, ,, | ,, 5050 | | 266 | 266 | 9′ Albatross Blake trawl | |
| ,, ,, | ,, ,, | ,, 5084 | | 918 | 918 | 9′ Agassiz | |
| ,, *mawsoni* | Berry (1917) | Australasian Ant. Exp. | | | 300–288 | | With *Pareledone*. |
| ,, *hippocrepium* | Hoyle (1904) | "Albatross" 3374 | | 1823 | 1823 | | Discrepancy, see p. 81. |
| ,, *glacialis* | Robson (1930) | "Discovery" 182 | | 152–273 | 152–273 | Otter trawl | |
| ,, *grimaldii* | Joubin (1920) | "Princesse Alice" 1334 | | | 1039 | Chalut | |
| ,, ,, | ,, ,, | ,, 1450 | | | 986 | ,, | |
| ,, ,, (?) | Massy (1916*a*) | "Investigator" 233 | | | 185 | | |
| | | ,, 332 | | | 279 | | |
| | | ,, 333 | | | 401 | | |
| | | ,, 361 | | | 540 | | |
| | | ,, 381 | | | 298 | | |
| ,, *wulkeri* | Chun (1914) as *umbellata* | "Michael Sars" 25 | | 1124 | 1124 | Trawl | The depths for specimens seems be "sounding depth." |
| | Grimpe (1920) | | | | | | |
| ,, sp. (juv.) | Hoyle (1912) | Scottish Nat. Ant. Exp. 295 | | | 2425 | | |
| ,, ,, | ,, (1905) | | | | 382 | Townet | |
| ,, ,, | ,, (1886) | "Challenger" | | | Surface | | Fragment. |
| ,, ,, | ,, (1904) | "Albatross" 3414, 3358 | | | 2232, 555 | | Fragments. |
| ,, ,, A | Robson (1924) | "Pickle" 525, 526 | | ? | 1400–1000 | Trawl | |
| ,, ,, B | ,, ,, | ,, 85 | | ? | 790 | Closing Net | On bottom. Only one depth given and Globigerina ooze taken at this. |
| ,, ,, | Berry (1912*a*) | "Albatross" 4325 | | 292 | 191–292 | 9′ Tanner beam trawl | |

| 1. | Authority. 2. | Cruise and station. 3. | Sounding (bottom depth) fms. 4. | Depth given for specimen (fms.). 5. | Gear. 6. | Remarks. |
|---|---|---|---|---|---|---|
| *? Grimpoteuthis* sp. | Hoyle (1904) | "Albatross" 3414 | | 2232 | | |
| ,, ,, (?) | ,, ,, | ,, 3358 | 555 | 555 | | |
| *Chunioteuthis ebersbachii* | Chun (1914) | "Michael Sars" 70 | 601 | 601 | Trawl | Depth or specimen = sounding depth. |
| | Grimpe (1916) | | | | | |
| ,, *gilchristi* | Robson (1924) | "Pickle" 526 | | 1400 | Reversible trawl | |
| *Cirroteuthopsis massyae* | Massy (1909) | Irish Fishery Survey | | 770–670 | Trawl | |
| *Froekenia clara* | Hoyle (1904) | "Albatross" 3358 | | 555 | | See p. 81 |
| *Cirrothauma murrayi* | Chun (1914) | "Michael Sars" 82 | | 1641 | | "M.W." |
| Opisthoteuthidae. | | | | | | |
| *Opisthoteuthis agassizii* | Verrill (1883, 1885) | "Blake" 260, etc. | ? | 291, 1058 | ? | |
| ,, ,, | Chun (1914) | "Michael Sars" 4 | 504 | 504 | Trawl | |
| ,, *depressa* | Ijima and Ikeda (1895) | Fisherman | | 250 | Long line | |
| ,, ,, | Sasaki (1920) | "Albatross" 4912 | 391 | 391 | 9′ Agassiz | |
| ,, ,, | ,, (1920) | ,, 4919 | 440 | 440 | | |
| ,, ,, | ,, (1920) | ,, 4969 | 587 | 587 | ,, | |
| ,, ,, | | ,, 5092 | 70 | 70 | 9′ Albatross-Blake trawl | |
| ,, ,, | Doflein (in Mayer '06) | | | 82 | | |
| ,, *medusoides* | Thiele (1915) | "Valdivia" 243 | | 218 | Trawl | |
| ,, *extensa* | ,, ,, | ,, 189 | | 420 | ,, | |
| ,, *persephone* | Berry (1918) | "Endeavour" | | 300–150 (4 stns.) | | |
| ,, *pluto* | ,, ,, | ,, | | 450–150 | | |
| Argonautidae. | | | | | | |
| *Alloposus mollis* | Verrill (1882) summary | "Fish Hawk" Stn. 880 | ? | 252 (? 225) | Trawl | See also p. 215 |
| | | 881 | ? | 325 | ,, | |
| | | 892 | ? | 487 | ,, | |
| | | 893 | ? | 372 | ,, | |
| | | 895 | ? | 238 | ,, | |
| | | 898 | ? | 300 | ,, | |
| ,, ,, | ,, (1884) | "Albatross" 2034 | 1346 | 1346 | Beam trawl | Young. |
| ,, ,, | ,, ,, | ,, 2036 | 1735 | 1735 | ,, ,, | Fragments. |
| ,, ,, | ,, ,, | ,, 2037 | 1731 | 1731 | ,, ,, | One arm. |
| ,, ,, | Hoyle (1886) | "Challenger"? | | "Picked up at sea" | | Fragment. |
| ,, ,, | Berry (1914) | "Albatross" 4095 | — | 290–286 | 8′ Tanner | |
| ,, ,, | Joubin (1920) | "Princesse Alice" 3031 | | Surface | | Fragment. |
| ,, ,, | ,, (1900) | ,, 844 | | ,, | | ,, |
| | | 848 | | ,, | | |
| ,, ,, | ,, (1895) | ,, 99 | | ,, | | ,, |
| | | 143 | | ,, | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Alloposus hardyi* | Robson (1930) | " Discovery " 288 | | 0–136 | Young fish trawl | |
| ,, *pacificus* | Sasaki (1929) | | | 200–150 | | |
| ,, sp. | Joubin (1929) | " Dana " 1215, v | | 322 | Ring trawl open | |
| *Alloposina albatrossi* | Hoyle (1904) | " Albatross " 3410 | — | 331(?) | Sigsbee (? trawl) | Station list (1894) gives 1429 fms.! |
| *? Heptapus danai* | Joubin (1929) | " Dana " 1349, iii | | 541 | Stramin net | |
| *Ocythoë tuberculata* | Degner (1925) | " Thor " 28*d* | | 109 | | See also p. 203 |
| ,, ,, | Joubin (1900) | " Princesse Alice " 637 | | " Au large de Monaco." | | |
| *Tremoctopus violaceus* | ,, (1929) | " Dana " 834 | | 27 | Open silk net | |
| ,, ,, | Berry (1914) | " Albatross " 9 stns. | | | | |
| | | 3799 | — | Surface (?) | Surface net | |
| | | 3878 | — | ,, | ,, | |
| | | 3926 | — | ,, | ,, | |
| | | 3929 | — | ,, | ,, | |
| | | 3930 | — | ,, | ,, | |
| | | 3931 | — | ,, | ,, | |
| | | 4010 | — | ,, | ,, | |
| | | 4011 | — | ,, | ,, | |
| | | 4086 | 283–308 | ,, (?) | ,, | |
| ,, ,, | Massy (1916) | " Terra Nova " 89 | | ,, | " 24 mesh net " } | ? Plankton net. |
| | | 129 | | ,, | " 18 mesh net " } | |
| ,, ,, | Degner (1925) | " Thor " 38*b*, 39*a*, 43*a* | | 35–13 | | |
| ,, ,, | Joubin (1920) | " Princesse Alice " 1768 | | 0–164 | Filet Richard à grande ouverture | |
| ,, ,, | Lo Bianco (1905) | " Puritan " 4 | | 54 | Closing net | |
| ,, *hyalinus* (?, p. 213) | Joubin (1900) | " Princesse Alice " 523 | | (Stomach of fish) | | |
| ,, ,, | Thiele (1920) | Deutsche Südpolar Exp. | | 1641 | Vertikalnetz | |
| ,, ,, | Chun (1915) | " Valdivia " 49 | | " In grossere Tiefe " | ,, | |
| ,, ,, (as *quoyanus*) | Lo Bianco (1905) | " Puritan " 42 | 1039 | 1094 | Closing net | Depth " Cave filato." |
| ,, ,, | Hoyle (1912) | " Scotia " tow net 59 | | Surface | Tow net | |
| ,, *atlanticus* (?) | Chun (1914) | " Michael Sars " 51, 53, 62 | | ,, | 51, 53 = " Catcher " | |
| ,, *scalenus* (?) | Hoyle (1904) | " Albatross " 3388 | — | ,, (?) | ? | |
| *Argonauta argo* | This form has been m | ainly found at the surface, but the followi | | ng record should be not | ed. | |
| | Verrill (1882) | " Fish Hawk " | | 365–64 | | Shells dredged. |
| ,, *hians* | Sasaki (1920) | " Albatross " 5081 | 500 | ? Surface | Intermediate net or Plankton net | See remarks (p. 81). |
| ,, ,, | Hoyle (1904) | ,, 3425 | — | 680 | Tanner trawl | Hoyle gives 680 fms. as depth; but Report (1894) gives 81 fms. |
| ,, *böttgeri* | Sasaki (*l.c.*) | ,, 4952 | 700 | Surface | Intermediate net or Plankton net | See remarks (p. 81). |
| Octopodidae. | | | | | | |
| *Benthoctopus piscatorum* | Verrill (1879) | Fishery schooner | — | 120 | ? | |
| ,, ,, | ,, (1880*a*) | ,, ,, | — | 200 | ? | |
| ,, ,, | ,, (1884) | " Albatross " 2035 | 1362 | 1362 | Beam trawl | |
| ,, ,, | Hoyle (1886) | " Knight Errant " 8 | — | 540 | ? | |
| ,, ,, | ,, ,, | " Triton " 9 | — | 608 | | |

| 1. | Authority. 2. | Cruise and station. 3. | Sounding (bottom depth) fms. 4. | Depth given for specimen fms. 5. | Gear. 6. | Remarks. 7. |
|---|---|---|---|---|---|---|
| *enthoctopus piscatorum* | Appellöf (1893) | Norwegian N. Atl. 124 | — | 350 | | |
| ,, ,, | ,, ,, | ,, ,, 359 | — | 416 | | |
| ,, ,, | Massy (1907–1909) | "Helga" 477 | — | 707–710 | Sprat net on trawl | |
| ,, ,, | Russell (1909–1922) | "Goldseeker" 19*a* | — | 563 | "Trawled" | |
| ,, ,, | Grieg (1927) | "Tovik" and "Armauer Hansen" 19 | — | — | From stomach of *Gadus callarias* | |
| ,, ,, | ,, ,, | "Tovik" and "Armauer Hansen" 113 | — | — | From stomach of *Gadus aeglefinus* | |
| ,, *levis* | Hoyle (1886) | "Challenger" 151 | — | 75 | | |
| ,, ,, (?) | Goodrich (1896) | — | — | 7 | | |
| ,, ,, (?) | Massy (1916*a*) | "Investigator" | — | ? | | |
| ,, *eureka* | Robson (1929) | — | — | — | | |
| ,, ,, | Hoyle (1912, as *tehuelchus*) | "Scotia" 118 | — | Shore | | |
| ,, *berryi* | Robson (1924) | "Pickle" 524 | — | 1200 | Reversible trawl | |
| ,, *sibiricus* | Løyning (1930) | Norwegian N. Polar Expedn. | — | — | Stomach of a walrus | |
| ,, *lothei* | Chun (1914) | "Michael Sars" 41 | 746 | 746 | Trawl | |
| ,, *hokkaidensis* | Sasaki (1920, 1929) | "Albatross" 5044 | 309–359 | 309–359 | Agassiz trawl | |
| ,, ,, | ,, ,, | ,, 5045 | | 359 | Albatross-Blake trawl | |
| ,, ,, | ,, ,, | ,, 5050 | 266 | 266 | ,, ,, | |
| ,, ,, | ,, ,, | ,, 5053 | 503 | 503 | ,, ,, | |
| ,, *thielei* | Thiele (1915) | "Valdivia" 160 | — | — | ? Shore | As *P. levis*. |
| ,, ,, (?) | ,, (1920) | Deutsche Sud Polar Expedn. | — | — | ,, | |
| ,, *januarii* | Hoyle (1886) | "Challenger" 122 | — | 350 | Trawl | |
| ,, *profundorum* | *id.* (1886) (as *januarii* pars.) | ,, 237 | — | 1875 | ,, | |
| ,, ,, (?) | Massy (1916*a*) | "Investigator" 222 | — | 405 | | |
| ,, ,, (?) | ,, ,, | ,, 332 | — | 279 | | |
| ,, ,, (?) | Sasaki (1920) | "Albatross" 4775 | 584 | 584 | Tanner beam trawl | |
| ,, ,, (?) | ,, ,, | ,, 4957 | 437 | 437 | Agassiz trawl | |
| ,, ,, (?) | ,, ,, | ,, 4973 | 600 | 600 | ,, ,, | |
| ,, *abruptus* | ,, ,, | ,, 4969 | 587 | 587 | ,, ,, | |
| ,, *magellanicus* | Robson (1930) | — | — | — | Shore | |
| ,, ,, | ,, (1930*b*) | "Discovery" WS. 97 | 79 | 79 | Otter trawl | |
| ,, *ergasticus* | Fischer (1892) | "Talisman" | — | 623–509 | "Dragage" | |
| ,, ,, | Joubin and Fischer (1907) | "Talisman" 84–5 | — | 470–454 | | |
| ,, ,, | Massy (1909) | "Helga" 331–489 | — | 385–720 | Trawl | |
| ,, *pseudonymus* | Joubin (1900) | "Princesse Alice" 719 | — | 875 | "Chalut" | As *O. levis* |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Teretoctopus indicus* | Massy (1916*a* as "*P. pricei* Berry") | "Investigator" 366 | — | 544 | | |
| | ? Winckworth (1926) | | | | | |
| ,, *alcocki* | Massy (1916*a*) (as *januarii*) | ,, 297 | — | 700–689 | | |
| ,, ,, | ,, ,, | ,, 343 | — | 609 | | |
| *Grimpella thaumastocheir* | Robson (1928) | ,, — | — | ? | | "Port Lincoln" (? shallow water). |
| *Eledone moschata* | Auctt. | Probably Jatta's "200 m." is the downward limit. | | | | |
| ,, *cirrosa* | ,, | Many records in water down to about 100 fms. | | | | |
| | | The following deep-water records are to be noted. | | | | |
| ,, ,, | Massy (1909) | "Helga" 366 | — | See col. 7 | Mid-water otter trawl | The record is given as "461 fathoms . . . mid-water otter trawl at 400 fathoms." This may mean that the animal was caught 61 fathoms from the bottom, |
| ,, ,, | Russell (1922) | "Goldseeker" | — | 464 | | This is var. *zetlandica* (Russell, p. 11). The range (*l.c.*) is given as 11–120 m.; but 850 m. is given on the same page! |
| ,, ,, (?) | Appellöf (1893) | Norw. Nordmeer Expedn. 34 | — | 587 | Trawl | Very young specimens (? pelagic). |
| *Pareledone charcoti* | Auctt. | "Pourquoi pas," etc. | — | Shore to 420 m. (Joubin 1914). | | |
| ,, *turqueti* | ,, | ,, ,, | — | 13 fm. (Joubin 1906) to 300 fm. (Massy, *l.c.*). | | |
| ,, *polymorpha* | Robson (1930*b*) | "Discovery" *passim* | | 8 m. to 149 m. (Robson). | | |
| ,, *harrissoni* | Berry (1917) | Australasian Ant. Expedn. X, XI, etc. | — | 358–270 fm. | Trap and trawl | |
| ,, *adelieana* | ,, (*l.c.*) | ,, ,, II | — | 300–288 | | |
| ,, *nigra* | Hoyle (1910) | Among rocks in shallow water. | | | | |
| ,, *antarctica* | Thiele (1920) | "Gauss" Stn. Deutsche Südpolar Expedn. | — | ? | | |
| ,, sp. | Massy (1916) (as *brevis*) | "Terra Nova" 42 | — | 40 | Agassiz trawl | |
| *Eledonella* | (Depths not given in original descriptions.) | | | | | |
| *Velodona togata* | Chun (1915) | "Valdivia" 249 | — | 409 | Trawl | |
| ,, ,, | Robson (1924) | "Pickle" 99 | — | 220 | Otter trawl | |
| ,, ,, | ,, ,, | ,, 162 | — | 240 | ,, ,, | |
| ,, ,, | ,, ,, | ,, 396 | | 250 | ,, ,, | |
| *Bathypolypus arcticus* | Auctt. | — | Very numerous records from "beach" to 843 fms. | | | |
| ,, *lentus* | Verrill, etc. | — | — | 603–120 | | |
| ,, *obesus* | ,, (1880) | Fishery schooner | | 300–160 | From stomach of a halibut | |
| ,, ,, | ,, (1882) | ,, ,, | | 150 | ,, ,, ,, | |
| ,, *sponsalis* | Fischer (1892) | "Talisman" | — | 683–509 | | See p. 300 for discrepancy in depths given. |
| | Joubin and Fischer (1907) | ,, 85–83 | — | 508–454 | Dragage | |
| ,, *saleorosus* | Sasaki (1920, 1929) | "Albatross" 5050 | 266 | 266 | Albatross-Blake trawl | |
| ,, ,, | ,, ,, | ,, 5029 | 440 | 440 | Agassiz trawl | |
| ,, *valdiviae* | Thiele (1915) | "Valdivia" 103 | — | 273 | Trawl | |
| ,, ,, | Robson (1924) | "Pickle" 63 | | 220 | Reversible trawl | } as *grimpei* |
| ,, ,, | ,, ,, | ,, 164 | | 380 | ,, ,, | |
| ,, ,, | ,, ,, | ,, 405 | | 470 | Otter trawl | |
| ,, ,, | Massy (1926) | "Pieter Faure" 18, 162 | — | 300 f. | Shrimp trawl | |

| 1. | Authority. 2. | Cruise and station. 3. | Sounding (bottom depth) fms. 4. | Depth given for specimen fms. 5. | Gear. 6. | Remarks. 7. |
|---|---|---|---|---|---|---|
| *Grimeledone challengeri* | Hoyle (1886) | "Challenger" 170*a* | — | 630 | Trawl | |
| ,, ,, (?) | ,, (1904) | "Albatross" 3393 | ? | 1020 | Tanner trawl | ? Discrepancy between Hoyle's data and station list. |
| ,, *verrucosa* | Verrill (1881) | "Blake" 305 | — | 810 | | |
| ,, ,, | | ,, 312 | — | 466 | | |
| ,, ,, | ,, (1884) | "Fishhawk" 1123 | 787 | 787 | ? | |
| ,, ,, | ,, ,, | "Albatross" 2050 | 1050 | 1050 | Beam trawl | |
| ,, ,, | ,, ,, | ,, 2051 | 1106 | 1106 | ,, ,, | |
| ,, ,, | ,, ,, | ,, 2077 | 1255 | 1255 | ,, ,, | |
| ,, ,, | ,, ,, | ,, 2102 | 1209 | 1209 | ,, ,, | |
| ,, ,, | Joubin (1924) | "Princesse Alice" 3437 | 787 | 797 | Chalut | |
| ,, *setebos* | Massy (1916) | "Terra Nova" (? Stn.) | — | — | In a rock pool | |
| *Thaumeledone brevis* | Hoyle (1886) | "Challenger" 320 | — | 600 | Trawl | |
| ,, *gunteri* | Robson (1930*b*) | "Discovery" 158 | 224–219 | 224–219 | Large dredge | |
| *Benthoteledone rotunda* | Hoyle (1886) | "Challenger" 157 | — | 1950 | Trawl | |
| ,, ,, (?) | ,, ,, | ,, 298 | — | 2225 | ,, | |
| ,, sp. ("*rotunda*") | Hoyle (1904) | "Albatross" 3398 | — | 1573 | "Sigsbee" | Discrepancy between Hoyle's data and station list (1894). |
| ,, *albida* | See p. 320 | | | | | |
| Vitreledonellidae | | | | | | |
| *Vitreledonella richardi* | Joubin (1918, 1924) | ?"Princesse Alice" 3223 | | 2899 | Chalut | |
| ,, *alberti* | ,, (1924) | ,, 3128 | | 0–1914 | Filet à 3 plateaux | |
| ,, ,, | ,, ,, | ,, 3131 | | 0–1914 | Filet Bourrée en vitesse | |
| ,, *ingeborgae* | ,, (1929) | "Dana" 1370 | ?1859 | 1094 | ?Stramin net (open) | ?Depth (Joubin). This may be station 1370(14) of the station list. |
| ,, *translucida* | Robson (1930*β*) | "Discovery" 273 | | 0–125 | Young fish trawl | |
| Eledonellidae. | | | | | | |
| *Eledonella pygmaea* | Verrill (1884) | "Albatross" 2099 | 2949 | 2949 | | |
| ,, ,, | Chun (1914) | "Michael Sars" 45,53,62 | 1567 (St. 53) | 1641–1422 | Beam trawl | "Catcher" (St. 53) |
| ,, ,, | Thiele (1915) | "Valdivia" 53 | | 1914 | Vertical net | 3000 m.w. |
| *Bolitaena massyae* | Robson (1924) | "Pickle" 87 | | 1014 | Closing net | "Net towed just clear of bottom." |
| ,, *massyae*, var. *purpurea* | ,, (1930*a*) | "Discovery" 86 | — | 0–547 | Tow net | |
| ,, *ijimai* | Sasaki (1929) | | | | | "Found with *Branchioceranthus imperator*." |
| *Iapetella heathii* | Berry (1912) | "Albatross" 4396 | 2228 | 2228 | 8′ Tanner trawl | |
| ,, sp. | Chun (1914) | "Michael Sars" 64 | | 1641 | "Catcher" | |
| ,, ,, | ,, ,, | ,, 92 | | 164 | | |
| ,, ,, | ,, ,, | ,, 92 | | 820 | | |
| ,, ,, | Berry 1914) | "Albatross" 4039 | 697–670 | 697–670 | 5½′ Blake beam trawl | |
| ,, ,, | Massy (1916) | | | 947 | | |
| ,, ,, | ,, ,, | "Investigator" 393 | 2000 | 400 | "Net" | |
| ,, ,, | ,, ,, | ,, 462*a* | | 475 | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| ,, sp. | Joubin (1920) | " Princesse Alice " | 2714 | | 765 | Filet Richard à grande ouverture | |
| ,, ,, | Degner (1925) | " Thor " ('08–'10) | 91*b* | | 875 | | |
| ,, *prismatica* | Hoyle (1886) | " Challenger " | 126 | | 770 | Trawl | |
| ,, ,, (?) | ,, (1904) | " Albatross " | 3414 | — | ?2232 | ? Tanner trawl | Discrepancy between Hoyle's data and station list (1894). See p. 81. |
| ,, *diaphana* | ,, (1886) | " Challenger " | 220 | | 1100(?) | | |
| | Joubin (1900) | " Princesse Alice " | 788 | | 2385 | Chalut | |
| ,, ,, | Hoyle (1904) | " Albatross " | 3366 | — | 1067 | | Discrepancy between Hoyle's data and station list (1894). See p. 81. |
| ,, ,, | | | | | | | ,, ,, ,, |
| ,, ,, | ,, ,, | ,, | 3415 | — | 1879 | | ,, ,, ,, |
| ,, ,, | ,, ,, | ,, | 3420 | | 664 | ? | |
| ,, ,, | ,, ,, | ,, | 220 | | 1897 | | |
| ,, ,, | Chun (1914) | " Michael Sars " | 35 | | 1423 | Trawl | |
| ,, ,, | ,, ,, | ,, | 53 | } 1430–1567 | 875 | " Catcher " | |
| ,, ,, | ,, ,, | ,, | 53 | | 1422 | (?) ,, | |
| ,, ,, | ,, ,, | ,, | 56 | 1777 | 164 | | |
| ,, ,, | Thiele (1915) | " Valdivia " | 12 stns. | | 2188–601 | All in Vertikalnetz | |
| ,, ,, | Massy (1916*a*) | " Investigator " | 273 | | 870–823 | | |
| ,, ,, | ,, ,, | ,, | 315 | | 705 | | |
| ,, ,, | Thiele (1920) | Deutsche Südpolar Expedn. | | | 1641 | Vertikalnetz | |
| ,, ,, | ,, ,, | ,, | ,, | | 727 | ,, | |
| ,, ,, | Sasaki (1920) | " Albatross " | 4956 | 720 | 720 | 9′ Agassiz trawl | |
| ,, ,, | Joubin (1920) | " Princesse Alice " | 1182 | | 1355 | Chalut | |
| ,, ,, | ,, ,, | ,, | 2168 | | 0–1094 | Filet Richard à grande ouverture | |
| ,, ,, | ,, ,, | ,, | 3028 | | 0–2789 | Filet Bourrée en vitesse | |
| ,, ,, | ,, ,, | ,, | 3039 | | 0–2002 | ,, ,, ,, | |
| ,, ,, | ,, (1924) | (?) ,, | 3082 | | 0–2188 | ,, ,, ,, | |
| ,, ,, | ,, ,, | ,, | 3086 | | 0–2352 | ,, ,, ,, | |
| ,, ,, | ,, ,, | ,, | 3128 | | 0–1914 | Filet à 3 plateaux | |
| ,, ,, | ,, ,, | ,, | 3131 | | 0–1914 | Filet Bourrée en vitesse | |
| ,, ,, | ,, ,, | ,, | 3205 | | 0–1641 | ,, ,, ,, | |
| ,, ,, | ,, ,, | ,, | 3215 | | 0–1094 | ,, ,, ,, | |
| ,, ,, | ,, ,, | ,, | 3217 | | 0–547 | ,, ,, ,, | |
| *Amphitretus pelagicus* | Hoyle (1886) | " Challenger " | 170 | | 520 | Trawl | |
| ,, ,, | Ijima and Ikeda (1902) | Fishermen | | | 312 | Long line | |
| ,, ,, | Thiele (1915) | " Valdivia " | 102 | | 984 | Vertikalnetz | |
| ,, ,, | Sasaki (1917) | | | | " Shore after a storm " | | |
| ,, *thielei* | Robson (1930*b*) | " Discovery " | 101 | | 0–218 | Tow net | |

## X. SYSTEMATIC TREATMENT.

### Order OCTOPODA, Leach, 1817.

Dibranchiate Cephalopods with eight arms. The visceral sac is suspended from the mantle in the nuchal and apical regions and by the median and lateral pallial adductors and the funnel depressors. The suckers are without a horny armature and (in most instances) peduncles. There is no oral funnel external to the lips. The shell is reduced to a single sub-apical or paired lateral vestige. The web is usually well developed and the oesophagus bears in most cases (and probably primitively) a crop-like expansion. The female genital ducts are usually paired and symmetrical.

The definition of the order given by Naef (1923, p. 655) included such features as the lack of a funnel-valve, occurrence of a branchial canal, etc. It is now shown that the Vampyromorpha have a valve, which is in all likelihood homologous with the valve of the Decapoda, that all the Octopoda do not possess a branchial canal of the *Octopus*-type, and that other characters originally thought to be diagnostic of the order no longer have that value.

It was for a long time customary to recognize only two major subdivisions of the order, viz. the Leioglossa and Trachyglossa of Lütken. The first included the forms now known as the Cirromorpha, the latter comprised the rest of the families constituting the order. In 1916 Grimpe proposed the names Cirrata and Incirrata for these groups, as being more appropriate. In 1921 Naef removed the Palaeoctopoda from the Incirrata and elevated them to the rank of a suborder. This threefold division was maintained by Grimpe (1922). In 1929 I removed the Vampyromorphae of Grimpe from the Cirrata and raised them to subordinal rank. At the time I felt justified in suspending judgment as to the status of the Palaeoctopoda. On examining with greater attention the single representative of that group I find it desirable to maintain Naef's suborder for it.

### Suborder I. VAMPYROMORPHA, Robson, 1929.

(EURYTRETA, VAMPYROMORPHAE, Grimpe, 1917; ODONTOGLOSSA, Naef, 1922 (Auctt. (where ?)); PROTOPINNATA, Sasaki, 1929; DICERATA, Joubin, 1929.)

Octopods with one or two pairs of fins and a single row of suckers accompanied by paired cirri on each arm. The suckers are pedunculate in some forms. A pair of velar filaments ( ? vestigial arms) is present in

nearly all the genera. The mantle-aperture is wide, and in some of the genera there is an adhesive apparatus of Decapod pattern. The ganglia of the central nervous system (as far as they are known) are distinct with separate brachial and superior buccal ganglia. The funnel has a valve. The radula is normally developed and the teeth are unicuspid. The shell-vestige is sub-apical and unpaired.

In his rearrangement of the cirrate Octopods (1917, 1922) Grimpe included the animals now placed in a distinct suborder, in the suborder Cirrata along with the Cirroteuthids and *Opisthoteuthis*. In 1929 (1929*a*, p. 484) I showed that *Vampyroteuthis* and its allies are the most archaic of the known Octopods and should be treated as a distinct suborder. This view has been strengthened by subsequent study.

Grimpe (*l.c.*) placed the five genera known to him in a family which he subdivided into two subfamilies

Vampyroteuthidae.

| | |
|---|---|
| Vampyroteuthinae. | *Vampyroteuthis.* |
| | *Watasella.* |
| | *Melanoteuthis.* |
| Laetmoteuthinae. | *Laetmoteuthis.* |
| | *Hymenoteuthis.* |

This classification was not very satisfactory. *Laetmoteuthis* was very imperfectly known and its fellow but little better. The radula of *Laetmoteuthis* is not figured, but Berry describes its rhachidian as three-cusped, which is a condition very unlike that found in *Vampyroteuthis*. The medians of *Hymenoteuthis* are unicuspid. *Laetmoteuthis* is devoid (apparently) of cirri, and *Hymenoteuthis* has them. On the other hand, they probably both maintain the archaic condition of having suckers all down the arms instead of restricted to the distal half or third. Berry does not, as a matter of fact, allude to the suckers in detail, but had they been restricted I am sure that he would have mentioned the fact. In 1929 Joubin, on the strength of the interesting material of the "Dana" Expedition, proposed an entirely new arrangement of the Octopoda.

OCTOPODA *Pteroti*—Acerata [no "tentacles"] Cirroteuthidae.
Dicerata [two "tentacles"] Melanoteuthidae.

A. Dipterata (two fins).

*Melanoteuthis,*
*Laetmoteuthis,*
*Danateuthis,*
*Retroteuthis.*

B. Tetrapterata (four fins).

*Vampyroteuthis,*
*Watasella,*
*Hansenoteuthis.*

*Hymenoteuthis* was not included in the list for some reason. Before we accept Joubin's classification we ought to inquire if the division into the two- and four-finned forms is justifiable. For a fundamental subdivision we require to know more details of the anatomy of all the forms involved. It should be noticed that one of Joubin's Dipterate forms (*Retroteuthis*) and one Tetrapterate (*Hansenoteuthis*) have an adhesive apparatus; that two of the Dipterate forms (*Laetmoteuthis* and *Melanoteuthis* have a fundamentally different type of central tooth, and that the former differs from *Melanoteuthis* in lacking cirri (see above) and having suckers all down the arms. The presence and absence of pedunculate suckers, a very important feature, again seem to cut across Joubin's divisions. For the present it seems very injudicious to make subdivisions of this group, though I think *Laetmoteuthis* (and possibly *Hymenoteuthis*) is very distinct from the rest. As for the validity of the genera, I am more than a little sceptical. I do not think it is possible to say as yet whether the position and type of light-organ and other differences, *e.g.* between *Melanoteuthis* and *Danateuthis* and between *Vampyroteuthis* and *Hansenoteuthis*, are of generic importance.

(a) *Special Morphology.*

Our knowledge of these interesting Cephalopods is at present incomplete. They have only become known to science since the beginning of this century, and our knowledge of the structure is principally based on the studies of Joubin (1920, 1929) and Robson (1929*a*), which were carried out on damaged and defective specimens. I have kept in the suborder forms like *Laetmoteuthis* and *Hymenoteuthis*, concerning which there is very little anatomical evidence, but they may eventually prove to be members of a distinct group.

*General build.*—The body is saccular or ovoid. In *Melanoteuthis lucens* and *beebei* it is small in comparison with the web and arms, but in *M. schmidti*, *Vampyroteuthis* and *Hansenoteuthis* it is elongate, ovoid, and is larger in proportion to the web and arms. The eyes are usually lateral in position. Those of *Hymenoteuthis* and *M. schmidti* may be dorso-lateral, while those of *M. lucens* are shown (? in error) (Joubin 1920, pl. V) as ventro-lateral. On the whole, one would not call the eyes very large. Those of *Vampyroteuthis* are rather small (or normal); those of *M. beebei* are distinctly big, being about half as long as the body. In the rest they are moderate to rather large ($\frac{1}{4}$–$\frac{1}{3}$ as long as the body). In *Hansenoteuthis* they are very prominent, and Brünmüller (*l.c.*, p. 321) definitely states that those of *Vampyroteuthis* are "gestielt." Berry (1912*a*, p. 273) notes a very marked asymmetry in *Hymenoteuthis*, the left eye being much larger than the right, a feature noted in other deep-sea Cephalopods (cf. *Histioteuthis*, Robson, 1924*a*, p. 608). Usually the head, body and arms form a compact mass; but in *Hymenoteuthis* there is a strong pre-ocular constriction and Brünmüller (*l.c.*) says that the "neck" in *Vampyroteuthis* is "deutlich abgesetzt." *Retroteuthis* shows a marked peculiarity in that the velar area is rotated over towards the dorsal region and its external tissues have become confluent with those of the latter. This peculiarity is found in a less marked degree in *Alloposus hardyi* (Robson, 1930*b*, p. 397) and *Heptapus* (Joubin, 1929*a*).

The suspension of the visceral sac and its relation to the head and mantle are virtually unknown. This is, of course, a very important item in Cephalopod morphology, the Decapoda and Octopoda differing usually in the suspension of the visceral sac. Sasaki (1929, p. 6) states that the *retractor pallii medianus* is " not developed " in *Watasella* and the septum is rudimentary. This ventral connection seems likewise to be absent in *Melanoteuthis* and *Vampyroteuthis* (Thiele, *l.c.*, pl. XCI, fig. 1). The absence of the ventral junction between mantle and visceral sac reminds us of the Decapoda (but cf. Sepiolidae). The arms are short or moderately long. They bear a single row of suckers, which are accompanied by filiform cirri, which alternate with the suckers. In *Melanoteuthis*, *Watasella*, *Vampyroteuthis* and *Retroteuthis* the suckers occupy about the distal half of the arm, *i.e.* they are more or less conterminous with that part of the arm which bears no web, the cirri usually commencing a little higher up and nearer the mouth. In *Hansenoteuthis* and *Danateuthis* the cirrhi (but not the suckers) approach much closer to the mouth. In *Hymenoteuthis* the distribution is not mentioned, but I assume that, had the suckers and cirri been in any way localized, Berry would have mentioned it. In *Laetmoteuthis* the suckers extend to the mouth, but there are probably no cirri (p. 112). In *M. beebei*, *Watasella* and *Danateuthis* the suckers are pedunculate, not sessile, and in *Retroteuthis* (Joubin, *l.c.*, p. 387) they seem sessile proximally and pedunculate distally, a highly interesting state, as it recalls that apparently found in *Palaeoctopus*. In *M. lucens*, *Vampyroteuthis*, etc., the suckers seem to be sessile. Although the pedunculate condition of the suckers is like that of the Decapods, it would be rash to conclude without a microscopical examination that the structure of the peduncles is identical in the two groups.

In five out of the eight genera which form this group (viz. *Melanoteuthis*, *Watasella*, *Danateuthis*, *Retroteuthis* and *Hansenoteuthis*) there have been recorded paired filaments arising from crypts in the tissues of the web situated in sector B on each side. These structures could not be found by Brunnmüller (1929, p. 319) in *Vampyroteuthis* and they are not mentioned in *Laetmoteuthis* and *Hymenoteuthis*. The general structure seems to be the same in all five genera. There is a subcutaneous pocket in the web with its orifice opening on the outer surface either at the edge of the latter (*Watasella*) or about in the middle (the other genera), and disposed with its lips parallel to the edge of the web. Rising from the base of this pocket is a filament with a thickish muscular base, which is continued downwards and is inserted into the base of the first arm. It usually lies coiled up in the crypt, but can obviously be extruded. The filament is variously shaped and is sometimes found provided with a long thread-like appendage. Its structure is simple. Its axis is occupied by a nerve, but there is no apparent end-organ. The nerve in question is said by Joubin (1929*a*, p. 373 and fig. 5) to be given off from the pedal ganglion between the roots of the first and second pedal nerves. In *M. beebei* I found its origin (1929*a*, p. 473, figs. 7–8) was from the pedal ganglion, but the pedal nerves are given off from the separate brachial ganglion, which is not mentioned by Joubin.* Joubin is of the opinion (*l.c.*, p. 378) that this filament " a la même valeur morphologique que le

* Joubin (fig. 5) shows the filament nerve and that of the first arm coming off the anterior surface of the pedal ganglion.

tentacule des Décapodes." The evidence for this conclusion is, of course, the innervation from the pedal ganglion. The resemblance to the Decapod tentacle is evidently heightened in his eyes by the fact that the appendage can be retracted and coiled up in its pouch. He is careful, however, to point out that the Decapod tentacle is situated in sector D (arms III–IV). I discussed the possible homology of these structures with the arms in 1929 (*l.c.*, p. 473–5) and on the whole agreed with Joubin's view, though I felt some difficulty in doing so. The evidence for and against the pedal nature of the filaments is as follows. (1) The filament is evidently produced by a branching or side-growth from the base of the first arm. It is not possible to be certain whether the root of the filament is independent or whether (as seems to be the case) it more or less comes off the first arm. In any case it goes right down to the circumoral muscular mass, and is (either directly or indirectly) an outgrowth from it. As such its brachial nature may be suspected. (2) The innervation has been already discussed (p. 93). Apart from the difference between the point of origin of the true pedal nerves and that of the filament nerve, I am satisfied that the latter arises from the pedal ganglion, and this fact may be an indication of the pedal nature of the filament, though, as I originally pointed out, innervation is not necessarily an infallible guide to the origin of the area or organ innervated (*l.c.*, p. 474). (1) and (2) may be taken together as strong evidence that the filaments are outgrowths of the pedal mass. (3) If the filaments are homologous with a pair of arms I find it difficult to understand their relation to the web. As they are now situated they are not attached to the web, but lie in cavities excavated in the latter. If they were originally arms we must imagine, on the assumption that the Protoctopod web was shallow, that the web grew upwards stretched from the first to the third arm and incorporated the (degenerate) second arm in its substance, leaving it free in its tubular pouch. (4) A matter of considerable interest but of some difficulty is involved, if we accept the filaments as vestigial arms and attempt to identify them with a specific pair of Decapod arms. By their position they should be homologous with the second pair of Decapod arms. Now it has been a matter of discussion whether the Octopoda are descended from a tentacle-bearing Decapod or from a more primitive ten-armed stage. Brock (1880, pp. 279–280) maintained the latter view, Pelseneer (1906, p. 331) and Dollo (*l.c.*, p. 114) the former. Abel (1916, p. 243) discussed the matter without being able to arrive at any certain conclusion. The fact is that our most useful source of information, viz. embryology, tells us nothing more than that the early embryo of the only type that has been fully investigated (*Octopus vulgaris*) has eight arms. If this number is eventually found to be characteristic of the embryos of all the members of the order, it may well suggest that the Octopoda are derived from an eight-armed stock and never passed through a ten-armed stage at all. On this view the homology of the filaments in the Vampyromorpha with true arms is rendered somewhat dubious. Nevertheless, from other morphological indications we have a rather strong reason for believing that the Octopoda had some affinity with fairly evolved Decapods. If this is true, as it seems likely, we have to assume that an arm (or tentacle) has been dropped out in the course of ontogeny. Pelseneer and Abel (*l.c.*) cite as evidence in favour of the

derivation of the Octopoda from tentacle-bearing Decapods, the fact that several Decapods (*Octopodoteuthis*, *Leachia*, etc.) have lost the tentacles. This interesting analogy, however, does not constitute proof. The question for solution may be briefly stated as follows (Text-fig. 12). If the Octopoda are descended from a tentacle-bearing form and have lost the tentacles themselves, the filaments cannot be interpreted as vestigial arms, the two extra appendages of the Decapod being accounted for by the lost tentacles. That the lost tentacles could have migrated forward to sector B and persisted there as the " filaments " is most unlikely. If, on the other hand, the Octopoda are derived from Decapoda with ten undifferentiated appendages, it is easier to accept the filaments as the missing arms (and to accept Naef's suggestion (1923, p. 655) that

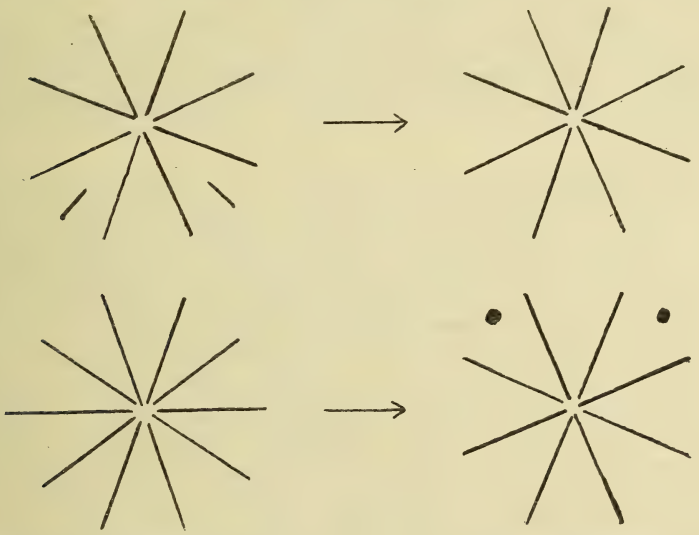


Fig. 12.—Diagram illustrating the relationship of appendages in Decapoda and Octopoda and the possible homology of the filaments in the Vampyromorpha (see p. 94).

In the lower figure on the right the black spots represent the filaments. The upper figures represent the descent of the Octopoda from a tentaculiferous Decapod; the lower shows their origin from a ten-armed form.

the Octopod third arms are homologous with the Decapod tentacles). On this assumption the characters which the Vampyromorpha and Decapoda have retained in common (valve, pedunculate suckers, etc.) were acquired before the tentacles were developed. I have presented all the facts that bear upon this question, though I do not feel they yield a final answer to our problem. Though I feel that the filaments are undoubtedly of pedal origin, I believe that their homology with arms is somewhat uncertain and that it is not altogether impossible that they may be secondary pedal outgrowths. There is no indication of the functions (if any) of the filaments. Joubin (1920, p. 26) hesitates between " une fonction olfactive ou quelque fonction accessoire de la réproduction." Sasaki (*l.c.*, p. 6) thinks they may be light-organs; but I hardly think this is a plausible suggestion.

The apical region is equipped with two pairs of fins in *Hansenoteuthis*, *Watasella* and *Vampyroteuthis*, and with a single pair in the other forms. The last-named form was described by Thiele as having a single pair; but Brunnmüller (*l.c.*) from an examination of the type has made it quite clear that there are two pairs in the latter. The fins are situated in most cases dorso-laterally, tending to be dorsal (especially in *Hansenoteuthis*). In *Laetmoteuthis* (Berry, 1914, Text-fig. 6) they seem to be lateral. The question of the nature and origin of the Octopod fins is discussed on p. 37, and it seems to me to be fairly certain that they are to be regarded as homologous with those of the Decapoda. In *Hansenoteuthis*, *M. schmidti* and *lucens*, *Danateuthis*, *Vampyroteuthis* and *Retroteuthis* pallial light-organs are found in various situations. They are also probably present in *M. beebei*. In practically all the forms so far described the tissues are alluded to as soft. In *M. beebei* they are certainly subgelatinous, and in *M. lucens* they seem to be even softer. The colour in *H. macrope* is a subtranslucent milky white, in *Laetmoteuthis* (when fresh) chocolate brown. All the others seem to be black or blackish purple.

*Skeletal structures.*

*Shell-vestige.*—Thiele (*l.c.*, p. 535) describes a thin glassy "Schalenhaut" in *Vampyroteuthis*. It is elongate "vorn kurz zugespitzt, nach hinten allmählich verschmälert, mit zahlreichen Konzentrischen Anwachslinien versehen." It is slightly asymmetrical, which Thiele regards as an "individuelle Unregelmässigkeit." I have examined another of the "Valdivia" specimens and can confirm Thiele's description. The shell-vestige in *Melanoteuthis lucens* is not described from direct inspection. Joubin says (1920, p. 23), "il est transparent et fait une forte saillie dorsale à la partie inférieure du sac viscéral; il a deux branches remontant vers les nageoires." In accordance with this impression he figures (Pl. XV, fig. 2) a hoop-like structure not unlike that of a Cirromorph. In *M. beebei* I succeeded in dissecting out the rather damaged vestige and found it to be a thin but tough cuticular plate. It is more or less oblong; its major axis is at right angles to that of the body. Its ends are thickened and in them are inserted the fin muscles. It is elevated in the centre, and there seems to be a median thickened ridge which projects somewhat apically. It is vaguely like the saddle-like vestige of *Cirroteuthis*, but is flatter and plate-like. The only other vestige known is that of *Hymenoteuthis*, in which it was not removed but was said to appear "more or less saddle-shaped, the posterior lobe rounded above, knob-like and very prominent." We thus find two distinct types of vestige in this group—a flat elongated plate vaguely recalling, by its shape and position, a Decapod gladius, and a broader more saddle-like structure that suggests the Cirromorph type. I ought to emphasize the fact that in *M. beebei* the organ like that of *Vampyroteuthis* is thin and laminar. In respect of its vestige it will thus be seen that this group contains elements recalling the Decapoda and others more akin to the Cirromorpha.

*Fin-supports.*—Brunnmüller (1929, p. 309) examined the solid bodies contained in the fins of *V. infernalis* and found they consist of a mass of elastic connective tissue of a "chordoid" nature. She points out that

it is interesting to find that the fin-skeleton is composed of this primitive (?) element and not of the more evolved chondroid tissue " dem direkt Vorläufer des Knorpels." I am not clear, however, as to her conclusions from this fact, especially as she calls these masses " Flossenstütze " and evidently wishes to compare them with the " Flossenstützen " of other Octopods. Now if she means by the latter the masses found by (*e.g.*) Meyer in the fin of *Opisthoteuthis*, the comparison is reasonable. Most unfortunately the term " Flossenstütze " has been used as recently as 1915–16 by Ebersbach and Grimpe for the shell-vestige, though Meyer (1907, p. 196) had already distinguished between the latter and the internal fin-skeleton. Actually Brunnmüller does not allude to this question. On the other hand, though she talks of the Octopod " Flossenstütze " and the possible significance of her discovery, she omits to mention the work of Meyer and Ebersbach on the structure and histology of the fin-skeleton in the Cirromorpha. As far as I can make out, the position and structure of the elastic connective-tissue pads in the Vampyromorpha and Cirromorpha are identical. The *cerebral cartilage* is scarcely developed at all in *Melanoteuthis beebei* and is " rudimentary " in *Vampyroteuthis* (Thiele).

The *radula* is known to occur in *Vampyroteuthis*, *M. beebei* and *schmidti*, *Laetmoteuthis* and *Hymenoteuthis*. In all five forms it differs quite markedly. However, *Melanoteuthis*, *Hymenoteuthis* and *Vampyroteuthis* agree in the fundamental simplicity of plan, there being a unicuspid rhachidian of simple shape followed by a slightly larger admedian more or less of the same form. *M. schmidti* differs from the others in its second lateral, which is a larger replica of the preceding tooth, whereas in the others there is a distinct indication of that specialization of the base of the third lateral characteristic of the Heteroglossa. *M. schmidti* is at once the most primitive and most like the Decapoda in this respect. *Laetmoteuthis* seems to be quite distinct from the other genera in its dentition, as its rhachidian is described as tricuspid and much larger than the other teeth. It is most unfortunate that no more is known of this form.

The *alimentary canal*.—The only information available is Joubin's slight account and drawing of the system in *M. lucens* and a few meagre references of Thiele's. Joubin shows no crop, but a very stout oesophagus, no salivary glands (?) and a bilobed liver. Thiele alludes to a crop-like expansion of the oesophagus in *Vampyroteuthis*. An ink-sac occurs in *Retroteuthis*, but has been noted in no other genus.

*Central nervous system*.—This was fairly fully described by me in *M. beebei* and rather summarily by Joubin for *M. lucens* and *schmidti*. It is not easy to compare our respective accounts. *M. beebei* certainly has a distinct brachial ganglion, as in the Decapoda, which is not shown by Joubin, the superior buccal ganglion is free and the cerebro-pedal commissure is still evident. The system in *M. beebei* shows a remarkable amount of diffuseness as compared with that seen in other Octopods.

The *pallial aperture* is always widely open. The funnel is usually large and prominent, though it may be short. In *M. lucens* it is more or less incorporated in the head. A valve is found in most of the genera. Berry does not figure it in his drawing of the funnel in *Hymenoteuthis macrope*.

The *funnel-organ* is present as a pair of ovoid, reniform or squarish pads. In *Danateuthis*, *Retroteuthis*, *Hansenoteuthis* and possibly in *Vampyroteuthis* there is a definite adhesive apparatus of the Decapod type consisting of a negative cephalic element and positive pallial one. It seems to be absent in *Melanoteuthis* and *Watasella*. The gills are only known in *Danateuthis*, *Watasella* and *Vampyroteuthis*. There is a maximum number of eight filaments aside. Joubin (*l.c.*, p. 381 and fig. 10) makes the highly interesting observation that the filaments in *Danateuthis* are free along their inferior border (" non réunies en un paquet " and cf. fig.), a condition more primitive than any found in the Dibranchia and resembling that seen in *Nautilus*. Sasaki and Thiele do not discuss this matter.

*Internal characters.*—Joubin speaks of a single lip in *Melanoteuthis lucens;* but he and Sasaki found two in *Watasella* and *Hansenoteuthis*. The mandibles seem in general to have no peculiar features except those of *M. beebei*, in which the gular lamella of the ventral mandible is short.

*Reproductive organs.*—There is no trace of hectocotylization in any known example, though Joubin's *Danateuthis schmidti* was a male. There is at present no account of the male organs, though from Joubin's casual remarks on *D. schmidti* one infers (1) that spermatophores are found and (2) there seems to be a long deferent canal. Sasaki (*l.c.*) states that both the oviducts are found in *Watasella*.

(b) *Systematic.*

Family 1. VAMPYROTEUTHIDAE, Thiele. With the characters of the suborder.

Subfamily 1. VAMPYROTEUTHINAE, Grimpe. The suckers occur only on a localized part of the arms, usually beyond the edge of the web. The radula has a unicuspid rhachis. Cirri always present.

Genus 1. **Vampyroteuthis,** Chun, 1903.

There are two pairs of fins (p. 98). The vestigial arms are absent. There is a pair of light-organs at the base of the fins. The suckers are probably sessile and are absent over the proximal region of the arms. The gill has eight filaments aside. The shell-vestige is elliptical in outline. An adhesive organ is present (?).

*Type of the genus.—Vampyroteuthis infernalis*, Chun, 1903.

This genus was first proposed by Chun in 1903 (1903, p. 88, text-fig.). He gave only a casual description, but it was figured and the name attached to the figure. He portrayed it as having four fins. In 1914 he referred to but did not describe (1914, p. 22) two damaged larvae from the " Michael Sars " expedition. In 1915 Thiele (1915, p. 534) described the " Valdivia " specimens in greater detail. According to Thiele the species has two and not four fins. In 1929 Brunnmüller made a fresh examination of the " Valdivia " specimens. She found in the type of the species

(Stn. 65) that there are two pairs of fins and a light-organ at the base of each fin. The other specimens (Stns. 85, 67) seem to have had their fins damaged. In the same year Joubin (1929, p. 369–371) alluded to but did not fully describe from the "Dana" spoils a specimen (more?) also having four fins. He also stated that the examination of the text of Chun-Thiele (1915) and a comparison of that work and the "Dana" specimens have shown that the Chun-Thiele description relates to two species at least. He says, "I have found among the 'Dana' Cephalopods specimens with four fins to which certain of the characters enumerated by Chun-Thiele are applicable, and other Cephalopods with two fins, to which certain of the other characters cited by those authors are applicable." In short, the *V. infernalis* of Thiele is not homogeneous. One form (with four fins, Chun, 1903) is the real *V. infernalis* and there remains one other form at least for separate treatment. The real *V. infernalis* was obtained in the "Dana" spoils (Joubin, *l.c.*, p. 371), but most unfortunately Joubin did not redescribe it, so that we might see which characters of those described by Thiele we should (in his opinion) attribute to this species. It is perhaps necessary to point out that the type of *V. infernalis* is among the "Valdivia" specimens (S. Atlantic), not among the "Michael Sars" (N. Atlantic) spoils, which Chun had not seen in 1903. It is most unfortunate that Joubin does not clear up the identity of the two-finned form which he asserts are included in Thiele's description of *infernalis*. He alludes to certain comparisons with *Danateuthis* (p. 375), saying "la description de Chun-Thiele du *V. infernalis* correspond en partie à ce que j'ai pu observer [in *D. schmidti*]." He does not, however, say if the "Valdivia" specimens, which are not attributable to *infernalis*, should be treated as varieties of *D. schmidti* or as distinct species. On p. 368 in naming *Danateuthis* he says "(ex *Vampyroteuthis* Chun-Thiele 1915)," yet he does not place "*Vampyroteuthis infernalis* Chun, (pars)" in the synonymy of *D. schmidti* (p. 375). If Thiele's description does contain matter relating to a form or forms distinct from the four-finned one, it seems very curious that Joubin should say his *Danateuthis* is "ex *Vampyroteuthis* Chun-Thiele" and yet not define the position of that element in Thiele's *Vampyroteuthis* which seems to resemble *Danateuthis*. In spite of this vagueness, however, Joubin is I think correct in his belief that Thiele's *Vampyroteuthis infernalis* contains more than one species.

(1) Plate XC, fig. 1, shows the inside of the web *black*.
„ 3, „ „ „ *brown*.
Text (p. 535) says "schokoladenbraun").
(2) Plate XC, fig. 1, has free arm-tips much shorter than in fig 3.
(3) Plate XC, figs. 1–2, show fins at one-third of the distance between eye and apex. Plate XCI, fig. 2, places them at one-eighth of the distance.
(4) Plate XC, fig. 1. Ventral sectors of the web are much larger than in Plate XCI, fig. 3; also the shape of the funnel differs.
(5) Plate XC, fig. 1, eyes red; text (p. 535) "purpurfarbig."
(6) Text (p. 536) indicates a fin light-organ in the example from Stn. 85. This is not mentioned in the others and is not figured.

I suggest that the species from Station 65 (originally figured in 1903 (1915, pl. XC, fig. 1 and ?2) is the true *V. infernalis*, and that the specimen from Station 85 (pl. XCI, fig. 3) be distinguished as a distinct species, on account of (1) the presence of fin light-organ, (2) the different shape of the funnel and (3) the size of the ventral web. It is possible that the third specimen (Stn. 67, ? = pl. XCI, fig. 2, "jungstes Exemplar") should be recognized as a distinct species also on account of the position of the fins. However, I do not deem it advisable to make these descriptions without seeing the specimens. In dealing with *Vampyroteuthis* it must be borne in mind that we do not know what characters in Thiele's anatomical description are applicable to *infernalis* and what to the proposed new species.

In the same work in which he discussed this matter, Joubin (*l.c.*, p. 388) described a new genus, *Hansenoteuthis*, which, like *Vampyroteuthis*, has four fins. He evidently thought that these two genera and *Watasella* have much in common, though he distinguished *Vampyroteuthis* and *Hansenoteuthis* by the fact that the former has neither "filaments" nor light-organs. As far as the latter are concerned, he is obviously in error (misled of course by Thiele's silence about fin light-organs in the type), in view of Brunnmüller's discovery (p. 99). The relation between *Vampyroteuthis* and the other genera is very obscure. It seems to be distinguished from *Danateuthis* by (*a*) its extra pair of fins and (*b*) its fin light-organs, and from *Hansenoteuthis* by the lack of the "filaments."

### Vampyroteuthis infernalis, Chun.

*Vampyroteuthis infernalis*, Chun (1903, p. 88, text-fig.).
,, ,, *id.* (1914, p. 22).
,, ,, Thiele (1915, p. 534, Pls. XC, figs. 1–3, XCI, figs. 1–5, text-figs. 67–70).
,, ,, Brunnmüller (1929, p. 302).

*Type.*—In Z.M., Berlin. (Holotype, see pp. 99–100.)

*Specimen seen.*—The type in Z.M., Berlin.

*Distribution.*—"Valdivia," Stn. 65 (1° 56′ S., 7° 40·6′ E., Cameroons-Congo R.,* in 656 fms.), vertical net; Stn. 67 (5° 6·2′ S., 9° 58·6′ E., off Congo R., ? depth), and Stn. 85 (26° 49·2′ S., 5° 54′ E., Walfisch Bay–Cape Town, in 2188 fms., vertical net. "Michael Sars," Stn. 57 (37° 33–11′ N., 29° 33–20′ W.), in 1094 fms. (wire), S.W. of the Azores; Stn. 51 (31° 20′ N., 35° 7′ W., S.W. of the Azores) in 1641 fms. (wire).

*Description.*—The body is of an elongate-ovoid shape. The head seems to be rather small with small pedunculate (?) eyes. The proximal part of the eye is broad and low, being shaped like a wide pot (Becher). I do not quite follow Thiele's description of the relation of the body—"der Mantel löst sich hinter den Augen vom Körper ab und buchtet sich in der Mitte ziemlich stark aus." † The animal has a very curious appear-

* I do not understand why this is alluded to by Thiele (*l.c.*, Pl. XC, explanation), as "in der Höhe der Capverden").

† This condition might mean that there was no nuchal fusion (p. 6); but I think Thiele would have emphasized such an important feature had it been present.

ance in Thiele's figure (Pl. XC, fig. 1), owing to the deep indentation just behind the eyes. The dorsal arms are rather longer than the ventral. Suckers are absent over the first half of the arm. Over the distal half, commencing at the level of the web, there is a small number (3–6) of small suckers uniserially arranged on each arm. They are wart-like and furnished with a small hole in the middle. There are about 6 pairs of cirri on the oral side of the first sucker. The web is extensive (Pl. XC, fig. 1) and must be about 85–90% of the arms in length. Thiele says, "ihre *grossere proximale Hälfte* wird durch eine Velarhaut verbunden!" The funnel is fairly prominent (Pl. XC, fig. 1). The fins are placed on the apical side of the middle-line. They are small, their length being about one-third of the head-width. They are parallel-sided and the width is about one-third of the length. The first figure of the animal showed a second pair of fins, as in *Watasella*, a fact subsequently confirmed by Brunnmüller. The colour of the external surface is black, the inner side of the web is chocolate-brown, the cirri whitish, the eyes purple (or red). The mantle-aperture is very wide. The funnel-organ consists of a pair of yellowish circular flat knobs (Warzen). Thiele does not allude to a valve.

*Light-organs.*—The skin contains a number of scattered whitish points which may be light-organs. There is on each side and in front of the fins a larger light-organ, the structure of which is described from the specimen from Stn. 67 (possibly a different species) by Brunnmüller. Thiele does not allude to the occurrence of "filaments." The ring-like buccal membrane displays 15 notches (Kerben). The mandibles have sharp rostra. The upper mandible is small, and, as in *M. beebei*, the rostral lamella has an external keel and is almost as deep as the palatal lamella. The inferior mandible is not described. The radula is well developed. The median tooth is unicuspid with a deep base; the admedian is of about the same size and has a slightly eccentric cusp. The second lateral is larger and with a thick heavy cusp and broadly oblong base. The third lateral is no longer than the second, and is relatively broader and shorter than that of *M. beebei*. Small ovoid (?) marginal plates are found. The cephalic cartilage is rudimentary. Thiele says there is a crop-like expansion of the oesophagus. The gills show 8 filaments aside. Thiele figures a thin "Schalenhaut." This structure, which I take to be homologous with the similar thin structure in *M. beebei* and to be a "shell-vestige," is long, narrow and elliptical, anteriorly somewhat pointed, posteriorly gradually reduced in width. It is marked with many concentric lines of growth and measures $9 \times 2{\cdot}5$ mm.

*Remarks.*—This form is distinguished from *M. schmidti* by the form of (1) its extra pair of fins, (2) eyes and (3) radula. From *M. lucens* it differs principally in (1) the shape of the body and (2) the fins. I do not, however, feel satisfied that these imperfectly preserved specimens are at all well known yet. Chun's N. Atlantic specimens referred to this species were not described. For the identity of Thiele's specimens see p. 100. The presence of an adhesive-organ seems to be indicated (Thiele *l.c.*, p. 535), but I cannot be certain about this.

### Genus 2. **Melanoteuthis,** Joubin, 1912.

There is a single pair of fins and a pair of " filaments " ( ? = vestigial arms). Cephalic (composite) and fin light-organs are present. There is no adhesive-organ, the radula resembles that of *Vampyroteuthis*, and a funnel-valve is present. The suckers usually commence at the edge of the web, the cirri about half-way or less from the latter to the mouth.

*Type of the genus.*—*M. lucens*, Joubin, 1912.

#### **Melanoteuthis lucens,** Joubin.

*Melanoteuthis lucens*, Joubin (1912, p. 1, text-figs. 1–12).
,, ,, *id.* (1920, p. 21, Pls. V, VI, VII, XV).
,, ,, *id.* (1929, p. 371).

*Type.*—Mus. Oc., Monaco. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Sargasso Sea in 1895 fms.; south of the Azores in 0–1094 fms.; 19° 04′ N., 65° 43′ W. (Caribbean Sea), ( ? depth).

*Description.*—The two specimens originally described were not in a very suitable condition for study, and several important points have to be stated subject to qualification. The body is said by Joubin to be short; the apex-eye length is, however (Pl. V), between 33% and 25% of the total length. The body is rather broadly oblong in shape. The head is not demarcated from the body. The eyes, however, are prominent. They are not very large, each being about 13% of the mantle-head area. The arms are in the order R 2 = 4.1.3, L 4.2. ? 1 = 3; but they are badly preserved. The suckers are all sessile. They commence at or slightly before the level of the web, and, in fact, occur only on the distal third of the arm. There seem to be at least two suckers on the oral side of the web margin. They are very small, round and widely open. Joubin says that the " cavité cylindrique est fortement creusée." This seems to suggest a condition not found in *M. beebei*. There seem to be 9–21 suckers on each arm, but the distal ones are so small that some may have been lost. The cirri are conical and end in a papilliform point. The longest are 1 cm. long. Joubin does not specify exactly where they start on the arms; but cf. Pl. XV, fig. 4. On the first left arm there are 14 pairs of cirri without suckers, on the second left 8 pairs without suckers, on the third right 6, and on the fourth right 5. The length of the web is not specified. It seems to be 60–40% of the arms; it is deeply incised in sector E. There seems to be (Pl. XV, fig. 4) a rather short brachial membrane on each side of the arm and a long lash-like extremity of the arm beyond this. The fins are subapical in position. They measure 40 × 22 mm. and are thus nearly twice as long as broad. The maximum width (Pl. XV, fig. 2) is about half-way along the fin. The posterior border is thick and rigid, the anterior thin and pliable. The maximum length of the fins is over $\frac{2}{3}$ of the interocular distance. The line of insertion is small, and the whole fin is paddle-like with a blunt point. The " tentacles " are found more or less in the same position as in *M.*

*beebei*. Each consists of a basal pigmented part which narrows to a filament and widens again. For a further discussion see p. 93.

A pair of large, simple light-organs of oval shape are found at the base of the fins close to the middle point of the insertion-line. No small or compound organs are found. The colour was almost entirely black when freshly caught. The tissues seem to have been soft and gelatinous. The mantle-aperture is wide. There is no trace of an adhesive-apparatus. The funnel is almost entirely imbedded in the tissues of the head, only its aperture projecting. The funnel-organ is not recognizable from Joubin's description. There is a transverse oval valve. The "shell-vestige" seems to have been flat and plate-like, to exhibit a marked median projection and to have two branches which extend towards the fins. The central nervous system is described by Joubin (1920, p. 29). The alimentary canal is roughly figured. From the figure one infers that there is no crop, that the stomach and coecum are both very small and the liver bilobed (see p. 12). The radula and mandibles are not mentioned.

*Remarks*.—This species differs from *M. beebei* in the shape of the body and fins, shape, etc., of the cirri and the form and setting of the suckers.

### **Melanoteuthis beebei,** Robson.

*Melanoteuthis beebei*, Robson (1929*a*, p. 469, text-figs. 1–8).

*Type*.—Coll. N. York N.H. Soc. (Holotype.)

*Specimen seen*.—The type.

*Distribution*.—Only known from the type locality, 4° 45′ N., 87° 0′ W. (between Cocos Island and the Galapagos Archipelago), in 0–750 fms. (Otter trawl).

*Description*.—The single specimen obtained is in a very fragmentary condition. Part of the web, the extremities of some of the arms and a portion of the apical area of the mantle are missing or badly damaged. The body is short and squat. The eyes are very large, and together must constitute nearly half the cephalo-pallial mass. The arms seem to have been about 60 mm. long or about 71% of the total length. They are equipped with suckers, which commence at the edge of the web. The exact number is rendered doubtful by the amount of destruction at the ends of the arms. There seem to have been 11–13 on each arm. The suckers are pedunculate and of an urceolate shape with slightly thickened rims. The walls are very thin, and there is no distinction into acetabular and infundibular areas. The cirri commence at about 10–12 mm. from the mouth and extend a considerable way up the arms. The exact extent of their distribution is uncertain. They measure up to 3·2 mm. in length. There are 5–6 pairs of cirri on the proximal part of each arm, which are not accompanied by suckers. The web is in a very fragmentary condition, being complete in three sectors only. As far as can be safely inferred, the longest remaining sector was 45% of the estimated arm-length.

"*Filaments*" (?).—One of these structures is found in sector B of each side. They seem to have been 15 mm. long, and to have consisted

of a thick pigmented basal part and a more slender unpigmented distal moiety. These structures are retractile into long crypts lying in the thickness of the web, and opening on the outside of the latter by slit-like orifices. The nature of these structures is discussed on p. 93. The *fins* measure 17 × 6·5 mm. The line of insertion represents the maximum width. They are more or less median in position.

*Light-organs.*—Traces of what appear to be light-organs are found towards the base of the second arms. The animal seems to have been black externally with the oral surface deep brownish purple. The body is highly gelatinous. The mantle-aperture is wide and extends halfway round the body. The funnel is prominent and has a wide base. It is supplied with a small but conspicuous valve, and there are inside two small squarish plates which may represent the funnel-organ. The shell-vestige is flat, roughly quadrangular and oblong, its major axis being at right angles to that of the body. It exhibits a median longitudinal ridge-like thickening in the main body axis, and has a vague likeness to the saddle-like structure seen in *Cirroteuthis*. The mandibles are tolerably well developed. The dorsal one has a narrow sharp rostrum, and the projection below the latter usually found in Dibranchiates is represented by the termination of an imperfectly chitinized fold. The ventral mandible has a very short gular lamella. The *radula* is well developed and has been fully discussed by me. It consists of 38 rows of 7 teeth. The central tooth is simple and has a tall, slender mesocone, the first lateral a similar but shorter cusp and a deep basal plate. The second lateral has an oblong basal plate, from which arises a long, gently-curved, blade-like cusp very like the third lateral. The latter is slender and has a slightly recurved tip. No definite traces of marginals could be found. The nervous system has been very fully discussed by me (see p. 97).

*Remarks.*—The other species of this genus known at present are not likely to be confused with it. *M. lucens* (see p. 102) differs in a large number of small particulars, which are alluded to in the description of that form. *M. schmidti* differs very markedly in the radula (cf. Joubin, 1929*a*, text-fig. 6, *c*, *d*), in the shape of the body, in the presence of only four (? more) suckers on the arms. Both these species are Atlantic forms, *M. lucens* being obtained in the Sargasso Sea, off the Azores and near the Leeward Is., and *schmidti* coming from the Caribbean Sea and S.E. of the Bermudas.

### **Melanoteuthis schmidti,** Joubin.

*Melanoteuthis Schmidti,* Joubin (1929*a*, p. 372, figs. 3–6).

*Type.*—(? Syntypes) In the Carlsberg Laboratory, Copenhagen (coll. "Dana").

*Distribution.*—Caribbean Sea (19° 04′ N., 65° 43′ W. and 17° 56′ N., 64° 50′ W.) and S.E. of Bermuda (28° 15′ N., 56° 00′ W.) in 1094–727 fms.*

*Description.*—The animal is very small, having a maximum length

* I have accepted Joubin's 2,000–1,330 m.; but it does not agree with the Station List records.

of 15 mm. The preservation is poor and the exact length uncertain. The body is long, the apex-eye length being rather under 50% of the total length. The apex is bluntly pointed. The eyes are very prominent. Joubin says they are large; but they do not seem particularly large in relation to the whole visceral mass. The arms are rather more than 50% of the total length. The exact number of suckers is not known. They seem to occur only beyond the web. Joubin found four on each arm (?), of which the inmost one was much larger than the rest. The cirri are transparent and paired as usual. There are practically none within the web. The largest are at the margin of the latter and are continued up the free part of the arm, diminishing rapidly in size. It seems from Joubin's fig. 3 that the suckers begin at about the same point as the cirri. The web is shorter than in *M. lucens;* but its exact size is unknown. The fins are narrow, with the sides more or less parallel, and having no basal constriction. Their length is rather more than half the interocular width. They are about four times as long as wide. The "filaments" are more or less in the same position as in *M. lucens*, but they are proportionately smaller and the basal part is thicker. Joubin (*l.c.*, fig 4) does not figure the terminal thickening seen in *lucens* (*id.*, 1920, Pl. VI, fig. 6).

*Light-organs.*—There is a pair of "composite" organs just below the "vestigial arms," and a larger pair just in advance of the insertion of the fins. The latter are round and reddish in colour. The skin is black except inside the web, where it is of a deep brownish violet. Neither the funnel nor its organ was described. *The radula.* The rhachidian is small, unicuspid, and seems to have a deep basal plate. The admedian is larger, but it and the following tooth seem to differ but little from the median, except in size and a slight eccentricity of the cusp. The third lateral is long and slender with a long basal plate. Joubin could not find any marginal plates. The third tooth is strikingly unlike that of *M. beebei.* The *central nervous system* was figured and described by Joubin.

*Remarks.*—Joubin says this species is externally very like *Danateuthis schmidti*, but that it is easily distinguished from it by the presence of the large light-organ near the fins. From *M. lucens* it is distinguished by (*a*) the form of the fins and "vestigial arms," (*b*) the relatively greater size of its head and body and (*c*) the shape of the visceral sac. From *M. beebei* it is at once distinguished by (*a*) the shape and size of the body and (*b*) the radula.

### Genus 3. **Danateuthis,** Joubin, 1929.*

There is a single pair of fins and a pair of "vestigial arms." Cephalic (composite) and simple light-organs are present. The suckers are pedunculate. The cirri reach two-thirds of the way to the mouth from the edge of the web. An adhesive-apparatus and valve are present.

*Type of the genus.—D. schmidti*, Joubin.

* *Danatenthis* [sic] (Joubin (1928, p. 441)) is obviously a mis-spelling.

**Danateuthis schmidti,** Joubin.

*Danateuthis schmidti,* Joubin (1929*a*, p. 375, figs. 7–12).

*Type.*—Carlsberg Laboratory, Copenhagen. (Holotype.)

*Distribution.*—" Dana " Stn. 1217, IV (18° 50′ N., 79° 07′ W., W. of Jamaica) in 908 fms. (? Joubin gives 1660 m., Stn. list gives 2500 m. wire out.)

*Description.*—The body is broadly oblong with a broad, rounded apex. The head is not demarcated by a furrow from the body. The eyes appear from the drawing (*l.c.*, fig. 7) to be asymmetrical. The smaller (? normal one) is moderately large. The arms are in the order 1.2.3.4, and the largest is 58% of the total length. The suckers are lacking over the whole of the web-area. It is not easy to determine the exact number. The largest is at the level of the web, from which point outwards they diminish in size until it is not possible to make them out. There are 13 shown in Joubin's figure (p. 379). The suckers are globular, rather flat and provided with a short peduncle, as in *M. beebei.* The cirri are arranged as usual in the group. They commence at about one-third of the way across the web. From the edge of the web they accompany the suckers as usual, and disappear at about the same level on the arms as the latter. The web seems to be equally developed in all its sectors, and to be rather less than 50% of the dorsal arms. The fins are attached rather in the dorsal region and much nearer the apex than to the eyes. They are rather long, well over half the interocular distance in length. Their width is $\frac{1}{2}$–$\frac{1}{3}$ of the length. The base is as wide as the middle part of the fin. The " filaments " are found, as usual, between the first and second arms on each side, perhaps rather lower down than in *M. beebei.* The " filament " itself is of uniform thickness in the type (unlike that of *Melanoteuthis*). The free part is bright yellow and reddish-yellow at the tip. In some specimens the slender terminal part seen in *Melanoteuthis* is found. The external surface is entirely black. The inner surface of the web is deep brown.

*Light-organs.*—(*a*) There are a number of small white nodules imbedded in the skin. Near the funnel these are placed close together. They are also found on the ventral surface of the eye and at the base of the ventral arms. (*b*) Grouped white nodules occur between the eyes on each side towards the base of the dorsal arms. Joubin (p. 376) specifically says these occur at the base of the dorsal arms, and they are so figured (fig. 7). The subsequent description (p. 382) seems to be contradictory and suggests that they occur in the interval between the third and fourth arms. These " composite organs " consist of closely approximated roundish nodules surrounded by a black border. These organs do not occupy the position of the dorsal organs placed close to the fins in, *e.g.*, *M. schmidti.* The mantle-aperture is very wide. Joubin (p. 380) describes what appears to be an adhesive-organ. The funnel has a valve and a funnel-organ composed of two oval masses. The funnel itself is wide but short. The mandibles are like those of *V. infernalis.* They are surrounded by a lip with 15 tubercles. The gills have 7 lamellae in each demibranch (see p. 98). The single specimen obtained was a

mature male. The little that can be made out as to the reproductive organs is mentioned on p. 98.

*Remarks.*—This seems to be a well-characterized form and is distinguished from the species of *Melanoteuthis* by the occurrence of an adhesive-organ.

### Genus 4. **Retroteuthis,** Joubin, 1929.

The surface of the web is fused with the tissues of the mantle in the dorsal region. There are two fins, and vestigial arms are present. Light-organs are found above the fins (?) and on the ventral surface. Both sessile and pedunculate suckers are found. There is an adhesive system and funnel-valve.

*Type of the genus.—R. pacifica,* Joubin.

#### **Retroteuthis pacifica,** Joubin.

*Retroteuthis pacifica,* Joubin (1929*a*, p. 383, text-figs. 13–16).

*Type.*—Carlsberg Laboratory, Copenhagen. (Holotype.)

*Distribution.*—Only known from "Dana" Stn. 1203–IX, 7° 30′ N., 79° 19′ W. (Gulf of Panama), in 1274 fms. (from Joubin's figures).

*Description.*—The body is ovoid, the maximum diameter being somewhat less than the apex-eye length. The eyes are large and prominent, but not excessively enlarged. The plane of the web has rotated through about 90°, so that the web has become attached to the dorsal surface of the mantle by its dorsal surface. The arms are in the order 4.1 = 3.2, and are 55% of the total length. Most of the suckers are sessile, but a few of the smaller ones are pedunculate. The suckers commence after the 6th or 7th pair of cirri (text, not fig.), *i.e.* near the level of the web. The first is the largest. They diminish gradually in size to where the arm becomes attenuated ("jusqu'à la naissance du fouet"). There are 7–8 sessile suckers on each arm. The cirri begin about 10 mm. from the outer lip. They increase in length till about the edge of the web, then decrease and "remain rudimentary up to the extremity of the arm." Joubin (fig. 13) actually shows them ceasing at an appreciable distance from the end of the arm. The web is very thin, probably equal in depth in all its sections, and is about 50% of the arms in depth. It is continued up each side of the arms for some way as a narrow membrane. The fins are placed rather behind the middle line. They are under half the interocular width in length, and their width is under half their length. The edges are sinuous. The "filaments" in their crypts are completely covered over by the adhesion of the web to the back, but it is of some significance that they are given access to the exterior by a kind of tunnel through the two juxtaposed epidermal surfaces (*i.e.* they evidently require to have access to the surrounding medium). The form of these tentacles is not described, and it is not apparent from the figure. Externally the animal seems to have been black. The oral surface of the web is of a very deep violet. On the ventral surface of most of the parts are to be found small white spots possibly of a luminous nature. Above the fins and towards the apex are figured two dorsal "light-organs."

The mantle-aperture is very wide. The siphon is far larger than in other members of the group (" du même genre " !). It projects beyond the eyes. It possesses an adhesive-organ. There is a thin triangular valve and a funnel-organ composed of two prominent ovoid rose-coloured plates. No other structures are described, but the presence of an ink-sac is mentioned. The single specimen was apparently a male.

*Remarks.*—The peculiar rotation of the velar area may only be a specific character. It occurs (p. 339) in *Heptapus* and *Alloposus hardyi* (but not in other species of that genus). Its origin has been discussed (Robson, 1930$\beta$), but there is little light to be cast on it as yet.

### Genus 5. **Hansenoteuthis,** Joubin, 1929.

There are two pairs of fins and a pair of vestigial arms. Cephalic (composite) and fin-light-organs are present. The cirri reach nearly to the mouth. There is an adhesive system.

*Type of the genus.*—*H. lucens,* Joubin.

#### **Hansenoteuthis lucens,** Joubin.

*Hansenoteuthis lucens,* Joubin (1929*a*, p. 388, text-figs. 17–23).

*Type.*—Carlsberg Laboratory, Copenhagen. (Holotype.)

*Distribution.*—" Dana " Stn. 1242 (24° 05′ N., 74° 36′ W., S.E. of the Bahamas), Stn. 1269 (17° 13′ N., 64° 58′ W., Leeward Is.), Stn. 1283 (14° 38′ N., 61° 16′ W., near Barbados), Stn. 1322 (27° 02′ N., 53° 39′ W., S.E. of Bermuda), in 583, 728, 911, 1094 and 1274 fms.

*Description.*—The description is based on the specimen from Stn. 1283. It is a very small example 35 mm. over all. The body is oval, its width being 60% of the apex-eye length. Its length is rather under 50% of the total length, and the interocular width is markedly greater than the body width. The eyes are very prominent, but they are not pedunculate. The arms are in the order 1.2.3.4, but they may be regarded as subequal. The suckers are found to commence just beyond the edge of the web. Joubin found there 3–4 very small ones, but could not say if there were more. The cirri commence quite near the mouth. There are five or six pairs inside the web. These increase in size to the edge of the web and then decrease outwards. The web is deeply incised in sector E, and seems to have the formula ABCDE (fig. 19). It is over 69% of the arms, and is continued up each side of the arms for a short distance. There are two pairs of fins. The lower (further from the apex; " supérieur " (Joubin)) pair is larger and more solid. It contains " un petit cartilage et des muscles." Joubin does not describe the former, nor does he say if it is continuous with the usual median fin-support. These fins are almost half the interocular width, narrow at the base and much broader at the distal third, after which they abruptly become narrower. The posterior border is more convex than the anterior. The apical pair is thin and soft and contains only some muscle fibres. It is somewhat shorter and narrower than the anterior pair, and (?) has a spatulate extremity (fig. 17).

*Light-organs.*—There is a pair of dorsal simple light-organs of circular

shape placed one at the base of each apical fin. A number of small simple organs are scattered over the body especially round the funnel on the base of the ventral arms. There is a pair of small compound organs between the eyes. Each is composed of about 40 small spherules lying on a special oval base. They are about 1·5 mm. in length and resemble those of *D. schmidti*. There is a " filament " on each side, placed as in other members of the group. It seems to have a thick base followed by a narrow portion, as in *M. lucens*. Joubin could not find a terminal thread-like part. The organ is yellowish in colour. The dorsal and ventral surfaces of web, mantle and head are black, the dorsal area being darker than the ventral, the difference in colour being clearly demarcated along the lateral line. The interior of the web is brownish-violet. The mantle-aperture is very wide. The funnel is short and scarcely projects from the surface. Its lateral " pillars " exhibit an adhesive-organ, which correspond with weak projections on the inner face of the mantle. Inside the funnel are two large yellowish reniform papillae, the components of the funnel-organ. Between them is a median " fossette." Joubin says (p. 391), " je n'ai pu constater s'il y a une languette mobile au-dessus de cette fossette." The mandibles are strong and very sharply pointed. They are surrounded by two lips, of which the inner one is lobate.

### Genus 6. **Watasella,** Sasaki, 1920.

There are two pairs of fins and a pair of " vestigial arms." There are no light-organs ( ?). The cirri extend from the base to the tip of the arms. The suckers are pedunculate, and there is no adhesive-organ. A funnel valve is present.

*Type of the genus.*—*W. nigra,* Sasaki.

#### **Watasella nigra,** Sasaki.

*Watasella nigra,* Sasaki (1920, p. 168, Pl. 23, fig. 1).
,, ,, *id.* (1929, p. 4, Pl. I, figs. 1–4, Pl. VII, figs. 1–2, text-figs. 1–2).

*Type.*—In U.S. Nat. Mus. (Holotype.)

*Distribution.*—Only known from the type locality, off Kii Province, Japan (33° 23′ N., 135° 37′ E.) in 544 fms. (" Albatross," Stn. 4977).

*Description.*—The only known specimen is very small, about one inch long. It is soft and " choroidal," the skin being quite smooth and black. In the dorsal and apical region of the mantle there is a longitudinal ovate patch of thin transparent skin. Sasaki queries whether this was not produced by accident. The body is long, and, with the head, constitutes nearly 50% of the total length. The eyes seem to be of moderate size, and the head is not demarcated from the body. The arms are subequal and just over 50% of the total length. The suckers and cirri are not well preserved. The former are pedunculate, as in *Melanoteuthis beebei*, etc. The aperture is minute, and they seem to be ten or more in number, though this is not certain. The cirri alternate with the suckers as usual and are crimson " in the distal parts." They seem to be 2–3 times as long as the diameter of the suckers. The suckers begin

at the distal half of the arm, and there are 10–12 cirri on the oral side of the first sucker. The " filaments " are found in sector B on each side. They are contained in long crypts, which open at the edge of the web. On one side the " filament " protruded some 8 mm. from the pouch. They are salmon-pink in colour and apparently of uniform diameter. The web is apparently equal in all its sectors and about 50% of the arms, extending up the sides as a brachial membrane. There are two pairs of fins, both of which arise rather near the median dorsal line and close to the oval patch described above. The fins are about twice as long as broad and their sides are more or less parallel. Their length is about a quarter of the interocular width. The funnel is roughly conical and projects but slightly. It contains a distinct semi-lunar valve and a funnel-organ consisting of two small ovate pads arranged with their long axes transverse to the main body-axis. The mantle-aperture is wide and extends half-way round the body. The gill is large. It is elongate and consists of 15 lamellae ($7\frac{1}{2}$ aside). The anus has two rudimentary valves. Sasaki does not allude to the ink-sac. The pallial septum is rudimentary and confined to the posterior extremity. The retractor pallii medianus is not developed. Both oviducts are present. The mandibles are strong and very large. The mouth is furnished with inner and outer lips. The radula is not mentioned.

*Remarks.*—Sasaki (*l.c.*, p. 6) makes a tabular comparison of this form with the Melanoteuthid forms known to him, and shows satisfactorily that it cannot be confused with them.

## Genus 7. **Hymenoteuthis,** Thiele, 1916.

There is a single pair of fins. Light-organs, vestigial arms and adhesive system seem to be absent. The cirri extend from the mouth to the tips of the arms. The radula shows more differentiation of the individual teeth than is found in the other genera. The shell-vestige is saddle-like (?).

*Type of the genus.—Cirroteuthis macrope,* Berry.

### **Hymenoteuthis macrope** (Berry).

*Cirroteuthis macrope,* Berry (1911, p. 589).
,, ,, *id.* (1912*a*, p. 273, Pl. XXXII, figs. 1–3, text-fig. 1).
,, ,, Grimpe (1916, p. 353).
*Hymenoteuthis macrope,* Thiele (1916, p. 4).
,, ,, Grimpe (1917, p. 320).

*Type.*—U.S. Nat. Museum. (Holotype.)

*Distribution.*—Only known from the type locality, " Albatross," Stn. 4393, in vicinity of San Diego, California, in 2113–2259 fms., on soft grey mud. (?) Indian Ocean (Massy 1916*a*).

*Description.*—The two specimens so far seen are rather small (the larger is 99 mm. over all), and subgelatinous in consistency. The body is long and with the head is about 50% of the total length. It is cylindrical in shape, the width being about 50% of the length. The head is wide and flattened with large prominent eyes which are apparently

asymmetrical, that of the left side being much the larger. The web and arms are separated from the head by a marked constriction. Berry compares the curious asymmetry with that seen in the Decapod *Meleagroteuthis*. I have myself recorded similar asymmetry in *Histioteuthis bonelliana* (1924*a*, p. 608). The arms are very fragmentary and their order, etc., is not known. The exact size and arrangement of the suckers are not given. They are apparently minute. The cirri are arranged "as usual" [? how], but are relatively large, "having the appearance of long pointed papillae." The web is in a very fragmentary state; but Berry thinks it was attached to the arms nearly, if not quite, to the tips. The fins are very long, about three-quarters of the interocular distance, and narrow. The width is nearly one-third of the length. They are "oar-like," and their greatest depth seems to be along the base-line. The colour is a "subtranslucent milky white; the umbrella and scant traces of epidermis remaining on the rest of the body a dark purplish brown." The mantle-opening is full and wide, reaching to a point just behind the eye on each side. The funnel is large, broad and little prominent. The funnel-organ is distinct and consists of two narrowly ovate white pads set slightly at an angle one to another. The mandibles are "black and horny, but not massive." The radula is present and well developed. From the figure (p. 273) the median seems to be small and unicuspid. The admedian is larger with a long slender cusp. The shape of the base is not clear. The second lateral is still larger and is not unlike that of *M. beebei* (p. 104), though the cusp is set nearly at a right angle to the line of the base. The third laterals, like those of *M. beebei*, are very slender. There are small squarish marginals. The shell-vestige was not removed, but seems to have been more or less saddle-like. "The posterior lobe" (?) is "rounded above, knob-like and very prominent."

*Remarks.*—The very short arms, clearly demarcated head, long body and narrow oar-like fins give this form a very characteristic appearance. The radula, in some respects, is like that of *Melanoteuthis beebei*, and possibly the "saddle-like" shell-vestige also, though the shape of the latter was determined only by palpation. There is no mention of the "vestigial arms" or of a funnel-valve. The latter is not definitely discernible in Berry's figure (Pl. XXXII, fig. 3), but it is just possibly represented by the pocket-like fold just above the funnel-organ. In having cirri along the entire length of the arm (see p. 93) this form seems to constitute a link with the next subfamily.

Subfamily 2. LAETMOTEUTHINAE, Grimpe. Suckers occur all along the arm. The radula with a multicuspid rhachis. ? Cirri absent.

Genus 8. **Laetmoteuthis,** Berry, 1913.

There is a single pair of fins. Light-organs, adhesive system and vestigial arms have not been reported. There seem to be no cirri. The suckers are sessile and extend from the mouth to the tip of the arms. The radula has a tricuspid median tooth.

*Type of the genus.—L. lugubris,* Berry.

**Laetmoteuthis lugubris,** Berry.

*Cirroteuthis*, (?) sp. Berry (1909, p. 418).
*Laetmoteuthis lugubris*, *id.* (1913, p. 563).
„ „ *id.* (1914, p. 275, Pl. XLIX, figs. 1–2, text-figs. 1–2).

*Type.*—In U.S. Nat. Museum. (Holotype.)

*Distribution.*—" Albatross " Stn. 3904 and 3898, off Mokapu Islet, Hawaiian Is., found at surface, and Pailolo Channel, Molokai in 284–258 fms.

*Description.*—The two specimens available are in a very fragmentary condition. The body seems to be large and rounded posteriorly. The eyes were probably large. The arms are long and appear merely " as thickenings " in the web. The suckers are " large." They are flattened and arranged in a single, occasionally somewhat zigzag row. Cirri are " indistinguishable." Berry thinks the possibility that the animal had cirri is remote; but he is alive to the possibility that they may have been restricted to the extremities of the arm and so lost in the destruction of the latter. The web is said to be " longer between the ventral arms," and is everywhere extensive, though very thin. In the table of measurements given by Berry (*l.c.*, p. 275) it is given as 100 mm. in E, 300 in A ! The fins are placed well back on the mantle. They are small, and their greatest width is just about half the length. They seem to be paddle-shaped. The colour is " a livid dark brownish slate with a somewhat bluish cast over the inner surface of the web in preserved specimens." When captured the animal seems to have been chocolate brown. The mandibles are large and black. With the exception of the sharp and powerful rostra, they are thin and comparatively fragile. The rostral lamella of the upper mandible is about half as deep as the palatine lamella. The gular lamella of the lower mandible is long and well developed. The radula is remarkably large and well developed. Unfortunately it was not figured by Berry. But he alludes to " the *tricuspid* medians " as being considerably the largest, two features in which the radula departs very markedly from that of the normal Vampyromorph type.

*Remarks.*—Berry believes that the larger of the two specimens obtained must have had a total arm spread of over 80 cm. He likewise believes that it is an abyssal form. It is a very great pity that the only two specimens known are both too fragmentary for further description.

## Suborder II. PALAEOCTOPODA,† Naef.

Littoral Octopods with fins, uniserial suckers, no web and no cirri (?). The ink-sac is present and there is a horseshoe-shaped (?) shell-vestige. Some of the distal suckers are pedunculate.

This group is represented by a single example, *Palaeoctopus newboldi*, obtained in 1846 from the Upper Cretaceous of the Lebanon. It was described by H. Woodward (1896, p. 229; 1896*a*, p. 567), and its affinities have been discussed by Dollo (*l.c.*, *passim*), Abel (1916 *passim*) and Naef (1921, 1922, 1923). I have recently made a re-examination of this interesting fossil (1930*a*, p. 544). The only definite pronouncement of recent years as to its status is that of Naef (1921, p. 36), who created for it a new suborder and pointed out (1923, p. 672) that it seems to occupy a position

between the Cirromorpha and Incirrata. This opinion was largely substantiated as a result of my recent study. I retained the suborder proposed by Naef, but after discussing the various characters individually and collectively I expressed the opinion that there is a marked preponderance of Incirrate characters, but that these are less definite than those found in the two other groups and that two of them, though not usually found in the Cirromorpha, occur in the rather enigmatic Stauroteuthid genus *Froekenia*. Finally I pointed out that the characters in which *Palaeoctopus* resembles the Vampyromorpha outnumber the Cirromorpha features, and that it rather seems to constitute a link between the Vam pyromorpha and Incirrata. I wish to modify this opinion, but there are certain points that require more elucidation. So far I have been able to make out nine features of taxonomic value, and these are given in the definition below. Two of these, however, require some discussion as, owing to the state of the fossil, I am not at all satisfied that divergent points of view may not be possible concerning them.

(1) I stated that no cirri were present, and this is true as far as the appearance of the profile of the arm is concerned. But in some Cirromorpha the cirri are so small or so highly retractile that I am not at all sure that they would necessarily figure in a fossil specimen. For this reason I am inclined to treat this feature as subject to doubt.

(2) Though the well-marked and characteristic thickening which I interpret as the shell-vestige is, I believe, correctly identified, I wish to correct the impression that my original description may give, that in *Palaeoctopus* the shell-vestige has exactly the same half-hoop shape as in some of the Stauroteuthidae. The vestige is by no means well preserved, and, though its general character is quite clear, owing to the vagueness of the impression in the apical region it is not evident whether it is really shaped like a half-hoop or whether it is thicker and broadly lunate. I do not think it could have been much thicker in the apical region, but it is very doubtful if it had a definitely half-hoop shape. It is a pity that the form of the vestige in *Melanoteuthis lucens* is not fully known, as Joubin (1920) described it as having two anteriorly directed horns.

(3) The absence of a web and the *Octopus*-like shape of the body are to a very large extent paralleled by the typical Cirromorph *Froekenia*, which has the general appearance of a young *Octopus macropus*, and I am not so much inclined now to treat these as essentially Incirrate characters. I believe that the following table illustrates the relationships of the various characters better than that which I originally proposed.

A. Vampyromorph characters.
   1. Fins.
   2. Uniserial Suckers.
   3. Pedunculate „ (some only).
   4. Ink-sac present (cf. *Retroteuthis* and p. 97).
   5. (?) Shell-vestige.

B. Cirromorph characters.
   1. Fins.
   2. Uniserial Suckers.
   3. Shell-vestige.
   4. Shape } resemble those of *Froekenia* only.
   5. Web }

Fig. 13.—† *Palaeoctopus newboldi*. U. Cretaceous. × 1·5.

C. Incirrate characters.

1. No Cirri (?).
2. Ink-sac present.
3. Shape.
4. Habitat (p. 116).
5. Uniserial Suckers (Bolitaenidae, *Eledone*, etc.).
6. Low Web (a few Octopodids, *Ocythoë*).

In my recent study (1930*a*, p. 547) I drew attention to the marked preponderance of Incirrate characters. On reviewing the data I cannot help feeling that, though they are numerically superior, the resemblance to the Incirrata are less important in themselves.

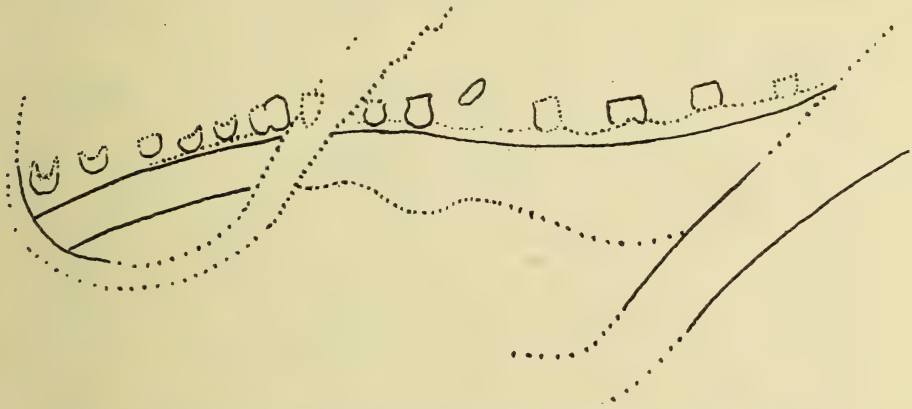


Fig. 14.—† *Palaeoctopus newboldi*. Portion of one of the arms showing approximate position of the suckers. × *c.* 3.

If we evaluate the uniserial suckers as common to all groups and treat the shell-vestige as likely to be either like that of the Cirromorpha or the Vampyromorpha and the cirri as doubtful, the general facies seems to be that of a generalized type combining more essentially Cirromorph and Vampyromorph characters. In fact, I only see one important reason for not treating it as a real generalized primitive Octopod, and that is our uncertainty as to the form of the shell-vestige. If the latter turns out to be of a half-hoop shape one of two conclusions may be possible: (1) that *Palaeoctopus* is a Stauroteuthid form which has re-acquired an ink-sac and pedunculate suckers and lost its deep web and cirri (?). This seems far less likely than the alternative, which would be to treat it as (2) a primitive form but having a shell-vestige that has come to resemble that of a Stauroteuthid by convergence. For the time being I treat it as a separate suborder having some affinity with the common stock of Cirromorpha and Vampyromorpha.

Family †PALAEOCTOPODIDAE, Dollo. With the characters of the suborder (p. 113).

**†Palaeoctopus,** Woodward, 1896 (*Calais*, Woodward). With the characters of the suborder.

**†Palaeoctopus newboldi**, H. Woodward.

(Text-figs. 13–14.)

*Calais Newboldi*, Woodward (1896, p. 229).
*Palaeoctopus newboldi*, *id.* (1896*a*, p. 567).
,, ,, Dollo (1912, *passim*).
,, ,, Abel (1916, *passim*).
,, ,, Naef (1922, p. 285).
,, ,, Naef (1923, p. 670 and foll.).
,, ,, Robson (1930*a*, p. 544).

*Type.*— In Brit. Mus. (Geol. Dept.). (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Upper Cretaceous (Senonian) of Sahel-el-Alma, Lebanon. (Only known from the type locality.)

*Description.*—The body is ovoid and saccular, the maximum width being a little behind the median line. The head is very small and clearly demarcated. The eyes are small but prominent. There are 8 arms apparently of unequal length. There is very scanty evidence of the occurrence of a web, and it was probably absent; but traces of what look like median keels are seen on some of the arms. The suckers are uniserial or arranged in a very wide zigzag. They are prominent and sessile proximally, but seem to be pedunculate distally. Situated with the anterior border well behind the median line there is a pair of triangular fins. These are one-half to one-third the maximum width of the body in length, and the greatest width, which coincides with the line of attachment to the body, is equal to the maximum length. In the apical region is found a wide horseshoe-shaped (?) shell-vestige, the exact form and extension of which are uncertain. The anterior borders of this reach about half-way from the apex to the eyes. There is a small elliptical ink-sac. Cirri seem to be absent.

*Remarks.*—(See above.) I am indebted to Dr. L. F. Spath for assistance in examining this fossil and also for the interesting information that the bed in which the fossil was found would have been laid down in only a few fathoms of water.

Suborder III. CIRROMORPHA, Robson (*Pteroti*, Reinhardt and Prosch, *Lioglossa*, Lütken, *Cirroteuthoidea*, Berry, *Cirrata*, Grimpe).

The radula is absent and the pallial aperture is reduced in width, ultimately becoming confluent with the aperture of the funnel. There are no vestigial arms, light-organs, adhesive-apparatus, or ink-sac. The shell-vestige is saddle-, hoop- or rod-like. The right oviduct is absent. The web is usually extensive and paired fins are present.

(a) *Special Morphology.*

The present state of our knowledge of this highly interesting group is not unsatisfactory. Complete accounts of the structure of *Grimpoteuthis umbellata* and *Chunioteuthis ebersbachii* were prepared by the late

Dr. A. Ebersbach, whose untimely death in the War deprived Cephalopod morphology of one of its most promising students. Meyer (1906) gave an equally exhaustive account of *Opisthoteuthis*. Reinhardt and Prosch (1846) and the present author (1924*a*, 1926*a*, 1930*b*) have described various parts of the anatomy of other species. On the whole, the structure of certain systems is fairly well known, though there is need for more knowledge on the central nervous system and alimentary canal.

*External features.*—The general shape and build of the majority of the Cirromorpha are those of a normal Octopod in which (*a*) the web is very much deeper, (*b*) the sides of the body carry fins, and (*c*) the mantle-aperture is reduced to a narrow slit surrounding the funnel or is actually united with the latter. The body is usually saccular or broadly oval, and the head is rarely marked off from it by the nuchal constriction so often seen in the Octopodidae.

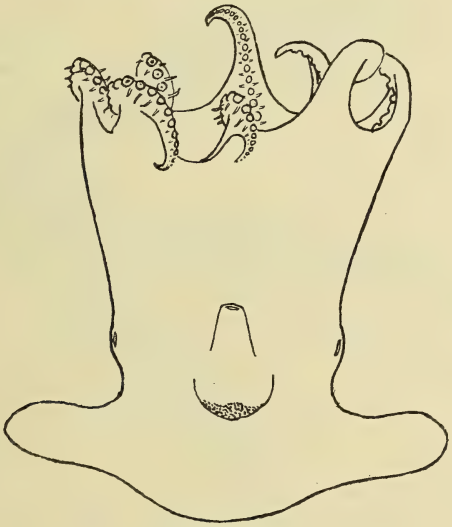


Fig. 15.—*Grimpoteuthis* sp. ("Sp. A," p. 155).

(*a*) The extensive development of the web may, I think, be regarded as secondarily acquired in the suborder. The web is very rarely developed in the Decapoda. It is true that in the Vampyromorpha it is usually 40–50% of the arms and therefore longer than in most Octopods. Nevertheless the union of the arms by an upwardly growing sheath of tissue must, I think, be regarded on embryological grounds as secondary in the subclass Dibranchia. In the early embryos of most Decapods and Octopods (Naef, 1928, *passim*) the arms originate as separate entities and continue to grow as such, and there is no trace of a web until a later stage. It is an open question, however, whether the deep web of the Cirromorpha indicates Vampyromorph affinities or whether it was acquired independently. A very interesting modification of the web is seen in *Cirroteuthis* (s.s.) and *Chunioteuthis*, in which the web occurs in two distinct parts, the primary web lying in the brachial interspace and the secondary web joining the primary web to the arms.

A somewhat analogous arrangement is found in *Histioteuthis* among the Decapoda, though in that form it is only the ventral arms that are involved. (For origin of the secondary web see p. 163.)

(*b*) The sides of the mantle are provided with a single pair of fins. These vary a good deal in size and shape and may be small and more or less apical, as in *Grimpoteuthis grimaldii*, or extend along the whole or a large part of the side of the body, as in *G. glacialis* and *G. mawsoni*. The actual origin of the fins has been a subject of some discussion, and to simplify the discussion in the general section (pp. 36–37) I give the details of this matter here. The full structure of the fins is well described by Ebersbach (*l.c.*, p. 381). They are characterized by the occurrence inside the muscular tissue of a flattish plate ("Stützgerüst") of elastic consistency and characteristic structure which was originally called the fin

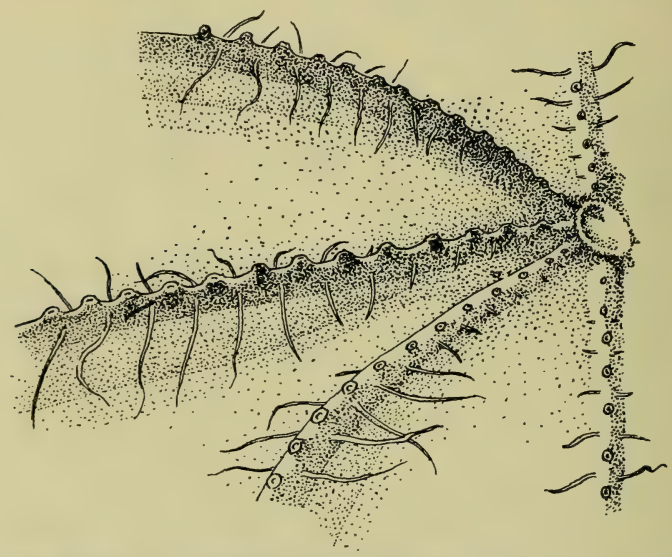


Fig. 16.—Portion of web of *Chunioteuthis gilchristi* showing intermediate web.

"cartilage" by Reinhardt and Prosch and Verrill. The structure is not, however, cartilaginous. The musculature at least in the forms described by Ebersbach is complex and, as he says (*l.c.*, p. 382), places the Cirromorph fin above that of the Decapod [in efficiency and variety of movement]. At first sight one would tend to accept the fins as an archaic feature and homologous with those of the Decapod. This seems to be the generally accepted view. I cannot, for example, find any indication in the writings of Naef that he believes that the fins of this group are secondary and not homologous with those of the Decapoda. Dollo, on the other hand (*l.c.*, p. 128), anxious to prove that *Cirroteuthis* is an "ultra-Pieuvre" or highly modified Octopodine, has tried to show that the fins of the Cirromorpha are secondary. His evidence is that "elles n'en [Decapod fins] ont, ni la Position, ni la Forme, ni la Structure," also that "elles ont un Squelette et une Musculature qui leur sont absolument propres."

This series of assertions rests not on personal examination or a critical study of the evidence, but merely on general remarks of Reinhardt and Prosch and of Meyer. (1) With regard to the position of the fins I do not think much importance can be attached to Dollo's view. I assume that he means that they are attached to the body not, as *e.g.* in *Loligo*, along the dorso-lateral line, but on the median lateral line. This position is, however, nearly attained in *Sepia*. (2) As to the form (? shape), little value is again to be attached to this, if we think of the difference between such Decapods as *Sepiola* and *Sepia*. (3) Dollo is on stronger ground as regards the structure. Both Meyer (*Opisthoteuthis*, *l.c.*, pp. 196, 197) and Ebersbach (*Cirroteuthis*, *l.c.*, p. 381 and foll.) show that in the Cirrata the musculature has a different arrangement from that found in the Decapoda. In addition there is an internal elastic core of special tissue (erroneously called the " Flossenknorpel " by various authors) which is not found in the Decapod fin. Meyer (*l.c.*) states that the musculature of *Opisthoteuthis* " gewährt der Flosse nicht nur eine Bewegung von oben nach unten wie sie bei den Flossen der Decapoden allein möglich ist, sondern auch eine Bewegung von vorn nach hinten." To these objections to the view that the fins of *Cirroteuthis* are homologous with those of the Decapoda, we might add a fourth. In some of the Decapoda the fins are provided with basal cartilaginous lamellae or rods, into which the transverse fibres (Querfasern) of the fin-musculature are inserted (cf. Meyer, 1913, fig. 15). This is not found in the Cirrata in which the musculature seems to be inserted into the lateral horns of the shell-vestige. I do not think there is any need to question the structural dissimilarity. Dollo, however, overlooks the fact that the Decapod fins exhibit some substantial modification (*Ctenopteryx*) and the possibility that the Octopod and Decapod fins may be homologous but yet have experienced some independent modification. In any case the matter cannot be settled until we know something more about the fin-structure in the Vampyromorpha.

(*c*) The *mantle-aperture*.—On this subject little need be said from the morphological point of view. As in *Nautilus*, the Decapoda and primitive Octopods the mantle-cavity is widely open, its progressive closure in the Cirromorpha must, I think, be secondary. A series illustrating this progressive closure would begin with *C. mülleri* (rather widely open) and passing through forms like *G. umbellata*, in which it is narrow, but there is still space on each side of the funnel, to *G. glacialis*, in which the mantle-rim tightly embraces the base of the funnel. Finally, in *Chunioteuthis* the funnel and mantle-aperture become confluent and there is a single aperture.

The general architecture of the Cirromorph body shows some marked difference from that of the normal Octopod. As is generally known, the latter diverges characteristically from that of the Decapod. The visceral mass of the Decapod is secured to the mantle along the whole of the mid-dorsal line and is usually free ventrally and in the nuchal region. In the Octopod the visceral mass is joined to the ventral part of the mantle by the median pallial adductor and is free dorsally, except in the apical and nuchal regions. In the Cirromorpha the dorsal section of the mantle-cavity, *i.e.* the space between the visceral mass and dorsal mantle, is largely reduced and more or less cut off from the ventral (branchial cavity) (cf. Meyer, 1906, p. 191; Ebersbach, *l.c.*, p. 374). In several forms in

which I have sought for the dorsal cavity it was not to be found. This, however, may be due to bad preservation. In *G. umbellata* and *glacialis* the median adductor is markedly reduced and in *C. mülleri* it is completely absent (Brit. Mus.). Brock (1880, p. 221) believes that this implies probably " ein sehr altes Verhalten " (? as in Decapoda and Nautilus) " welches durch eine . . . vollständige Verwachsung des oberen Mantelrandes mit dem Kopf . . . compensiert wird." Actually in *C. mülleri* the mantle-aperture is fairly open and it is in forms that still have a median adductor that the closed mantle-cavity is found. On this account I am not inclined to believe that the cephalo-pallial union is functionally associated with the absence of the median adductor. As to whether the latter feature is primitive or secondary, I admit that the forms with a (reduced) adductor might be held to be primitive and *C. mülleri* (no adductor) as more evolved. But *C. mülleri* has other primitive traits, and both the absence of the adductor and the widely open mantle-aperture look suspiciously like a primitive condition. The very far-reaching modification of the body-plan in the Opisthoteuthidae is discussed on p. 45.

The funnel in most of the Cirromorpha is fairly prominent, but its musculature seems on the whole to be poorly developed. The arms are usually subequal and deeply sunk in the swollen tissues of the web. The suckers are always uniserial and usually small. Sometimes, as in *G. albatrossi* and *Opisthoteuthis* (Sasaki, 1929, pp. 8, 11), there is a discontinuous enlargement of some of the suckers in the male; but it is by no means universal (*e.g.* in *G. glacialis*, which is only known from a male specimen, the suckers are all small). The suckers are sessile. Sometimes the inferior chamber is weak and its walls thin, at others it is strong and well developed (*G. glacialis*). In *Opisthoteuthis* (Meyer, *l.c.*, fig. p. 200) the acetabular chamber alone is muscular. There is no certain evidence as to the number of suckers in the ancestral Octopoda and Decapoda, but as in the early embryo the suckers seem to arise in a single row (cf. Naef, 1928, Pl. XVI, fig. 4 and text-fig. 119) we can safely assume that the single row in the Cirromorpha is a primitive character. Down each side of the arm and usually alternating with the suckers there is a row of *cirri*. The structure of these organs has been investigated by Meyer (*l.c.*, p. 201). The function is unknown. Meyer believes that they are sense-organs; Abel (1916, p. 27) considers that they are tactile. Hoyle (1886, p. 56) thought that they might either be tactile or used, like cilia, for creating food currents. More or less similar cirri are found in at least one genus of Decapoda (*Cirrobrachium filiferum*, Hoyle, 1904, p. 28). One is also reminded of the lateral processes on the hectocotylized arm of *Alloposus*. Possibly the cirri are homologous with the transverse ridges (" Seitenbrücke ") on the lateral membranes of the Decapod arm, though I hardly think it likely.

*Internal anatomy.*

*The Alimentary System.*—The mouth is surrounded by circular inner and outer lips. Within these lie the mandibles. These structures do not show any conspicuous deviation from the normal Dibranchiate type. Sometimes (as in *G. glacialis*) they are delicate and the palatal lamella tends to become somewhat abbreviated. On the whole, however, the degeneration seen in the radula has left the mandible quite

untouched; nor is the musculature of the mandible weakened in the forms with which I am familiar. In fact, Ebersbach (*l.c.*, p. 389) alludes to the strength of the jaw-muscles. In the majority of the Cirromorpha the radula (and in *Chunioteuthis ebersbachii* the complete lingual system as well) is entirely absent. *G. umbellata*, according to Ebersbach, still exhibits "einen, wenn auch stark rückgebildeten und offenbar völlig funktionslosen Rest der Reibplatte. Es waren nur noch drei Längsreihen winziger, höchst einfach gebauter Zähnchen vorhanden." The submaxillary or subradular gland is present and seems to be normally developed. The anterior salivary glands are present in *Chunioteuthis ebersbachii* and very small in *G. glacialis* and *mülleri*, and the posterior glands are entirely absent in those forms, *Ch. ebersbachii*, *G. albatrossi* and *Opisthoteuthis*, in which all the salivary glands are absent. In *G. umbellata* alone are the posterior glands present as a median unpaired mass. In this form Ebersbach (*l.c.*, p. 392) found that the usual anterior salivary glands are absent and are replaced by intrabulbar (intrapharyngeal) "buccal glands" (apparently homologous or even identical with the anterior salivary glands). Intrabulbar salivary or buccal glands are found in the Sepiidae and Sepiolidae among the Decapoda (Wülker, 1910, p. 38 and foll.), and in the Loliginidae and Egopsid Teuthoidea they occupy an intermediate position. The oesophagus is normal in structure in all the forms examined. There is no trace of a crop in *G. glacialis*, *Ch. gilchristi* and *ebersbachii*; in *C. mülleri* (B.M.) and *G. umbellata* there is a very moderate enlargement of the oesophagus in the place usually occupied by the crop, and in *Opisthoteuthis* (Meyer, *l.c.*, p. 206) there is a gradual enlargement of the posterior end of the oesophagus which may or may not be analogous to the true crop. The significance of the absence of the crop in some Cirrata and its partial reduction in others is very obscure. At first sight, and certainly with least difficulty, it might be explained as a loss. It is true we have no means of deciding if the series of modifications seen in the Cirromorpha is one of regression, but one is entitled to suspect that it is of this nature. Nevertheless, *Nautilus* has a moderate crop (*i.e.* not sharply delimited) and the Decapoda none at all. If we think the series in the Cirromorpha is regressive, we may hold that their affinities in this respect are with the Incirrata; if we think they originally had no crop and are gradually acquiring it, we shall believe that they show affinity in this respect with the Decapoda. The *stomach* is, in general, like that of the Octopodidae. There is usually a well-developed median muscular area, the thick walls of which project into the lumen. The inner wall is provided with a thick and strong cuticle. Longitudinal ribs are found in *G. glacialis*, in which the grinding apparatus is very strong. The coecum is well developed in most forms. In *G. glacialis* it is very large. It usually shows no trace of spiral twisting, though some effects of this are seen in *G. umbellata* (Ebersbach, *l.c.*, text-fig. 11). The inner surface of the coecum, which is usually thin-walled, is thrown into a number of ridges (*G. glacialis* and *umbellata*), and its function is no doubt essentially absorptive. The functions of the stomach and coecum as grinding and absorptive organs respectively are indicated markedly in *G. glacialis*, in which the small, highly muscular and strongly cuticularized stomach contrasts with the bulky thin-walled coecum.

The coecum is succeeded by the intestine, of which in some forms the first third is dilated to form a "third stomach." This is very clearly differentiated in *Opisthoteuthis*. In the walls of the third stomach of this form are numerous glands communicating with the cavity of the gut. A third stomach is found in *C. mülleri*, *G. umbellata*, *Ch. ebersbachii* and *gilchristi*. The liver is usually, as in the Octopoda, a large compact ovoid body opening into the coecum by paired hepatic ducts. In the figure of *G. albatrossi* given by Sasaki (1929, fig. 3*a*) the liver has the appearance of being divided into right and left lobes. I do not know if this is more than the effect of the usual indentation in which the alimentary canal lies; but it is quite marked and recalls the bilobed condition found in Decapods. A similar bifurcate condition is found in *Chunioteuthis ebersbachii* (Ebersbach, *l.c.*, p. 394), and in *Opisthoteuthis* Meyer describes the liver as bilobed as distinguished from "zweizipflig." (For a discussion on this point see p. 39 and cf. *Melanoteuthis lucens*.) The intestine shows some variation in length and in the course taken towards the anus. In *Chunioteuthis gilchristi* and *Opisthoteuthis* the alimentary canal forms a simple loop, the oesophagus and stomach forming the dorsal section, after which it bends in the apical region and the intestine returns direct as the ventral sector to the anus. In *Grimpoteuthis albatrossi* and *G. glacialis* the intestine bends on its course and forms a secondary loop in accordance with its greater length. There is never any trace of an ink-sac. The anal valves are absent or rudimentary.

It is very difficult to formulate an explanation of the causes of the very marked changes in the Cirromorph alimentary canal. At the present moment we have insufficient information as to the group as a whole; but what we know is enough to awaken our curiosity. The following characteristics, however, are shared in common by nearly all the specimens examined.

1. The mandibles and their musculature are normal and strong.
2. The radula is absent.
3. The crop is absent or reduced.
4. The posterior salivary glands are absent in all the known forms save one.
5. The stomach is muscular and seems to retain its function of a grinding-organ.
6. There is very often a third (? absorptive) stomach.

This series of characters was subjected to a preliminary examination by me (1926*a*, p. 1348), and I pointed out that, from what is known of the contents of the gut, these animals do not restrict themselves to organic débris but swallow prawns, etc., whole. In *G. glacialis* I found large pieces of Polychaetes. Of course it is not possible to say if they are carrion-eaters or if they eat living prey. The food they eat obviously has to be torn up, ground down and subjected to the usual digestive processes. How then are we to account for the absence of the radula and crop and the development of a third stomach?

(a) *The loss of the radula.*—The radula is usually regarded as a masticatory organ. Griffin (1900, p. 159) has questioned whether the radula (in *Nautilus*) is really used for scraping and breaking up the food, and seems to believe that it is more useful in the swallowing process. Miss A. Bidder tells me that in the stomach of *Loligo* she found large pieces

of fish that had simply been cut across roughly by the mandible, and she has suggested that the radula may be a mechanism to assist bolting the food. If there is any functional significance in the absence of the radula, it should be that the Cirromorpha do not need either to masticate the food or to have any assistance in bolting it. This might be explained on the ground that the food was already broken up and somewhat reduced. Perhaps the absence of the crop would fit in with this explanation, if the food could be easily passed down to the stomach without being temporarily stored in the crop owing to the ease and rapidity with which such débris (being already broken up) would be ground in the stomach. This explanation, however, seems to me to break down for three reasons. (*a*) The crop is absent in the Decapoda in which, from what we know of the feeding-habits, and, if the above explanation is valid, it should be necessary. (*b*) The strong muscular stomach does not look like an organ for reducing already disintegrated food. (*c*) Finally, the débris which I have found in the stomach of several forms is by no means in a soft and broken-down condition. Ebersbach's experience (*l.c.*, p. 394) is worth quoting *in extenso*. "Den Drüsenmagen fand ich an beiden Tieren leer vor, wahrend die Muskelmagen und bei *C. umbellata* auch der Oesophagus mit kleinen Krustern vollgefüllt waren. Diese waren nur schwach beschädigt . . ." In short, both Ebersbach and I find unbroken remains in the stomach (cf. also p. 23). We are plainly not in a position to explain the peculiar features of digestion in this group, nor even to decide whether a given feature like the lack of a crop which the Cirromorpha share with the Decapoda, or the absence of posterior salivary glands which they share with *Nautilus*, has any functional meaning. This matter is alluded to more comprehensively on p. 29.

*Respiratory Organs.*—The gills lie as usual on each side of the median line in the pallial cavity. They exhibit two distinct and characteristic series of modifications.

(a) *Reduction in size.* The primitive Cephalopod gill no doubt bore numerous filaments. In *Nautilus pompilius* there are 65–55 a side (Griffin, *l.c.*, p. 141), and in *Ommastrephes* about 50. Among the Cirroteuthidae *C. mülleri* alone shows a number of filaments (8–9) that approaches the unspecialized Octopod number (10–12). In the others the filaments may be no more than 3–5. In the Opisthoteuthidae we find 3–4. The size of the filaments is also small, and the total area of the gill usually diminutive. As I have pointed out (1930*b*, p. 378), the reduction in size may be to some extent compensated by the more numerous plications.

(b) *Arrangement of the filaments.*—As is well known, the lamellae of the gills in *Nautilus* are entirely free at their extremities. In the Dibranchia they become attached to the dorsal wall of the mantle-cavity along their afferent borders. Along the line of junction with the mantle is developed the so-called "branchial gland." In the Decapoda the ctenidium still exhibits a primitive condition like that of *Nautilus* (Schäfer, 1904, Pl. 1, fig. 1), in that the opposed filaments are still widely separated. In the Octopodidae, however, the extremities of the filaments are approximated and almost in contact along the top of the branchial gland. Between them a cavity, the branchial canal, is developed. In none of the Cirromorpha so far described or known to me are the filaments dis-

posed as in the Octopodidae. There are two distinct types of gill in the group. (1) *C. mülleri* (Prosch and Reinhardt, *l.c.*, Pl. IV, fig. 2; Robson (MS.)), and apparently in the form of *G. umbellata* described by Ebersbach (*l.c.*, text-fig. 14) there is a plainly biserial arrangement, but the filaments diverge widely and more or less enclose the branchial gland, and there is no trace of a branchial canal. This is the condition found in *Sepia*, *Loligo* and other Decapods (Meyer, 1913, fig. 36; Schäfer, 1904, Pls. 1 and 2). This resemblance to the Decapod gill is very surprising. What is, however, perplexing is that in the specimens of *G. umbellata* on which Dr. Ebersbach worked, and which were kindly loaned to me by the Bergen Museum, I quite failed to find this arrangement. The filaments are arranged as in Joubin's figure (1900, Pl. III, fig. 5), *i.e.* according to the plan described in the following paragraph. Either Ebersbach was mistaken, which is not at all likely, or else the description of the gills is based on a specimen different from those seen by me and possibly referable to another species. (2) In other forms (e.g. *Chunioteuthis ebersbachii* and *wülkeri*, *G. glacialis*, *G. albatrossi* (?), *G. umbellata* (Joubin), *Opisthoteuthis*) the filaments have a totally different orientation. The gill is not in the form of two sets of filaments hanging down on the opposite sides of a main axis and disposed parallel to each other, but is, to use Ijima and Ikeda's excellent simile, like the half of an orange in which the segments of the fruit are represented by the filaments. In short, what has happened in these Cirromorpha is that the gill has become flattened and the filaments have come to lie parallel to the main axis, instead of at right angles to it. The result is that a transverse section of the branchial gland does not cut the filaments longitudinally but transversely. What the significance of the changed position of the filaments may be is not easy to decide. The close connection of the filaments with the branchial gland is lost and the gill is deprived of its peculiar structural support. In its place in *Opisthoteuthis* (Meyer, *l.c.*, p. 216) we find a cartilaginous skeletal support of the gill and its filaments. These supports are not apparently found in the Cirroteuthidae. If Meyer's account of them in *Opisthoteuthis* is correct the position is very remarkable, as branchial skeletons are found in certain Decapoda, *e.g.* in *Sepia* (Burne, 1899, p. 55 (cartilage)) and *Loligo* (Williams, 1909 (?), p. 64 (" chitinous nature ")). Schäfer (1904, p. 8) contradicts the earlier statement of Frey and Leuckart as to the occurrence of a branchial cartilage in the " Loligoneen " [sic]. The presence of this structure, however, is quite clearly established in *Sepia*. One is irresistibly reminded of the chitinous supports in the Lamellibranch gill.

*The Vascular System.*—The heart is as usual a muscular tube lying more or less transversely to the main body-axis. In *Ch. ebersbachii* three main arterial trunks arise from it, the aorta cephalica, posterior and genitalis, as in most Cephalopoda. In *G. umbellata*, on the other hand, as in some Oegopsida, the genital artery has lost its independent origin and has become a branch of the posterior aorta. As regards the rest of the system, an important feature must be mentioned. We owe to Ebersbach a very full account of the vascular system of *G. umbellata* and *Chunioteuthis ebersbachii* and a comparision of that arrangement with that described by Grimpe (1913) in *Eledone*. It is true that we have but these accounts to base our own upon, but the differences are so pro-

found that I believe we may take them as characteristic of the two groups. The outstanding and highly significant difference consists in the fact that in the Cirrata the venous system is very largely " enclosed," *i.e.* it consists of vessels throughout the major part of its extent. In the Octopodidae, on the other hand, a large part of the system consists of large sinuses into which the main venous trunks open directly. " Das Venensystem . . . weist zahlreiche Eigenheiten auf, die allerdings zum grossen Teile durch die hochgradige Rückbildung der Sinus bedingt sind und die oft eine gewisse Ähnlichkeit mit dem Venensystem der Decapoden hervorrufen " (Ebersbach, *l.c.*, p. 441).

*The Central Nervous System.*—The ganglionic mass, which we usually call the " brain " in these animals, attains in the Cirromorpha a very

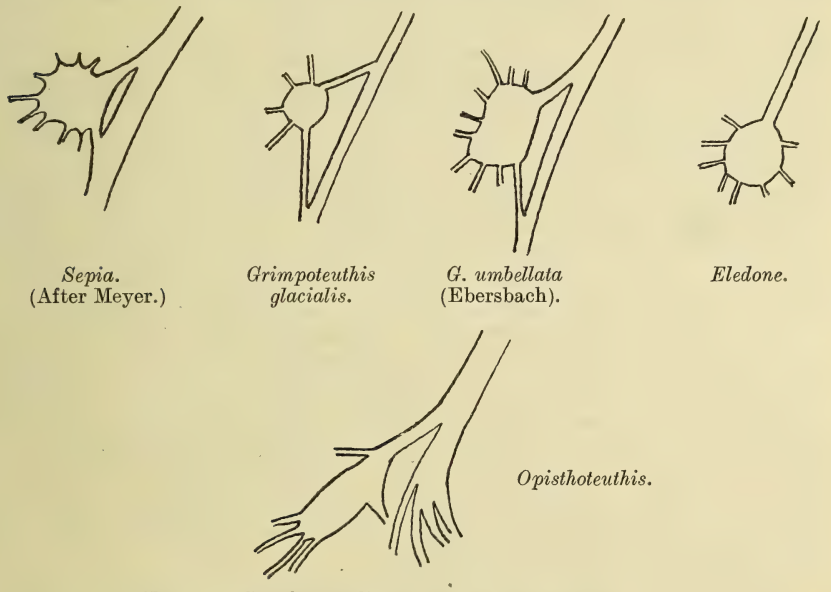



Fig. 17.—Ganglion stellatum of various Octopoda.

high degree of concentration, equalling or even surpassing that found in the Octopodidae. It has been summarily discussed by Pfefferkorn (1915, p. 525). The following points are to be noted :—

(1) There is no trace of the separate brachial and superior buccal ganglia found in the Vampyromorpha (*Melanoteuthis beebei*) and Decapoda.
(2) The superior buccal ganglion is still seen as a distinct mass in *Grimpoteuthis umbellata*, as in the Octopodidae and Argonautidae.
(3) The superior and inferior buccal commissures reach the most extreme degree of shortening (Pfefferkorn, *l.c.*, p. 521).
(4) As opposed to the specialized features seen in (1)–(3) the Cirromorpha possess paired suboesophageal ganglia (Pfefferkorn, *l.c.*), a characteristic unique in the Dibranchia and not found in the Bolitaenidae, etc.

There is a remarkable likeness between the Decapoda and Cirromorpha in the position of the stellate ganglion, which lies on a side branch of the pallial nerve (text-fig. 17). Pfefferkorn (p. 522) considers that the Cirromorpha are specialized in some respects, archaic in others, and " dürften eine Seitenfamilie der Octopoden darstellen." He thinks they may have branched off from the main evolutionary series (as indicated in the central nervous system) which commences with the Eledonellidae (the least specialized) and passes through the Octopodidae to the Argonautida.

*Sense Organs.*—The eyes in some forms tend to be large. In *Opisthoteuthis* the possession of " Sockelpigment " in the retina is, according to Meyer (*l.c.*, p. 259), evidence that it functions in nearly lightless regions. Ebersbach (*l.c.*, p. 474) says that *Cirroteuthis* agrees with *Opisthoteuthis* in its structure (except that the musculature is weaker), so that, though it seems to inhabit greater depths, its eyes are not modified accordingly. In *Cirrothauma* the eye is profoundly modified. It is devoid of lens, ciliary body and iris, and the optic ganglion is reduced " to a faint thickening of the optic nerve " (Chun, 1914, p. 27). The statocysts of *Ch. ebersbachii* resemble those of the normal Octopods in having a connective tissue " Wulst " in their cavity. In *G. umbellata*, on the other hand, the wall of the capsule bears six projections (Zapfen) like those of the Decapod statocyst, instead of the characteristic connective-tissue swelling found in the other Octopods. The olfactory organs lie on each side of the funnel. Unlike those of *Octopus* and *Eledone*, in which they are cavities in the skin, they are represented by swellings in this group.

*Coelom*, etc.—The coelom of the Cirrata shows the typical Octopod condition, viz. the reduction of the originally capacious genito-pericardial cavity (*Nautilus*) to the cavity of the gonad and that of the appendage of the branchial hearts which is joined to the gonadial coelom by the water canals or aquiferous ducts. In *Chunioteuthis ebersbachii* the condition is typical. In *G. umbellata* and *Opisthoteuthis*, however, the process of reduction is carried to further extremes, and the water-canal on the right side is partly atrophied and does not communicate with the gonad (Meyer, *l.c.*, Pl. XIV, fig. 18).

*Reproductive System.*—As in all the Dibranchia (except *Calliteuthis*) the male organs are single and consist of the original left member of the pair. In the Octopoda generally the female system usually displays the original condition of a pair of oviducts. However, in the Cirromorpha the left one alone remains (as in *Spirula* and the " Myopsida ").

(a) *Male System.*—A very elaborate description of this system in *Chunioteuthis* and *G. umbellata* is given by Ebersbach (*l.c.*). For the sake of brevity I have condensed his observations as far as possible. In *G. umbellata* there is a rather short vas deferens which leads on to a series of three seminal vesicles. These follow one after another, and the deferent canal then enters the side of a large oblong penial complex consisting of three accessory penial glands of which one (the largest) occupies the apex of the mass, the other two the base, from which the penis projects. At the point of union with this complex the deferent canal bears a small accessory gland. The rather simplified figure of Prosch and Reinhardt (*l.c.*, Pl. IV, fig. 5) shows a more or less similar system. In *Chunioteuthis* the same type of system is found with certain differences. There seems to be no extra-penial accessory gland (Rangierdruse), the seminal vesicles

are longer and the vas deferens shorter and thicker. The shape and arrangement of the three penial glands is different, the apical gland being smaller and the distal ones larger. In both forms Needham's organ is found as an elongate, thin-walled sac closely applied to one side of the penial complex, and at first sight seemingly confluent with the latter. The distal section of the vas deferens, where it enters the penial complex, passes between Needham's organ and the apical member of the complex and enters the former at its anterior quarter. According to Ebersbach (p. 413) the point of junction of the deferent canal with Needham's organ occupies a more anterior position in *umbellata*. Neither of the two forms studied has an appendix. *G. glacialis* (cf. Robson, 1930*b*, fig. 5) stands intermediate between *Chunioteuthis* and *G. umbellata*, as it has an extra-penial accessory gland, but the penial complex resembles that of *Chunioteuthis*. The proximal vas deferens is very much longer than in either of the other forms. The arrangement of the system in *C. gilchristi* seems to be simpler. There are three long vesiculae which run straight into the penis, round which the penial accessory glands are disposed in a circle. In *Opisthoteuthis* we notice some differences from the above, especially in the apical accessory penial gland, which is much smaller than its fellows. Meyer states specifically (*l.c.*, p. 230) that no spermatophores are found in *Opisthoteuthis*. Ebersbach mentions spermatophores in the form with which he worked, *e.g.* in the third section of the vesicula he found "rudimentär" spermatophores (*l.c.*, p. 412). I could find none in *G. glacialis*.

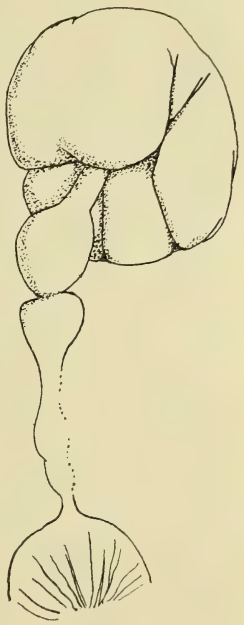


Fig. 18.—*Cirroteuthis mülleri*. Reproductive organs (♂). × 3·5. Brit. Mus.

(b) *Female Organs*.—These are not described for *Chunioteuthis* or *G. umbellata*. The only Cirromorpha in which they have been figured are *C. mülleri* and *G. albatrossi*. The oviduct and vagina are both very short in the former, particularly the vagina, which is almost globular. Both are longer and narrower in *albatrossi*, and the oviduct bears a small enlargement near the middle. The spermoviducal gland is very large, and its two divisions are very clearly seen. In *Opisthoteuthis* the oviduct is longer and thinner than the vagina, and the spermathecae are also large, the distal part being markedly larger than the proximal. In *G. albatrossi* the ovarial eggs are probably about 30% of the body in length, and in *C. mülleri* and *Opisthoteuthis* they look about the same size.

*Comparison of the Male System with that of other Cephalopoda*.—Ebersbach (*l.c.*, p. 416) regards the male system of the Cirrata as having been evolved from that of the Incirrata. He thinks that it is the end term of a progressive series that begins with the "Oegopsida" and passes through the "Myopsida" to the Incirrata, *Argonauta* and the Cirrata being the most evolved in this respect. The basis for this opinion consists in the belief that sundry features in the Cirrate system are the result of a general process of reduction and simplification. These features

are as follows : (*a*) The proximal vas deferens is remarkably abbreviated. (*b*) The first vesicula seminalis, as in the Octopoda and unlike that of the Decapoda, is small. (*c*) The accessory gland (prostate), which in the Decapoda is large and attains its maximum development in the Octopodidae, is reduced. (*d*) The coecum is entirely absent. (*e*) Needham's organ is shortened and has lost its " Wulst." I freely admit that, in the absence of more conclusive evidence than that adduced by Ebersbach, this view is reasonable. The shortening of the vas deferens is unequivocably evidence that a process of reduction is at work. Perhaps the reduction of the accessory gland is more satisfactorily explained as the result of atrophy than as a rudimentary condition. I think, however, that Ebersbach should have noted that in the Cirrata the system shows some measure of resemblance to that of *Nautilus*. The Decapod and Octopod system at its full development is characterized by extensive diverticula from the main channel. In *Nautilus* these are absent, and in the Cirrata the diverticula are slight and insignificant, except in the case of the penial glands. Two facts must make us hesitate before making a too facile comparison with the Tetrabranchiate system. (1) The penial glands are reasonably to be derived from the characteristic penial diverticle of the Octopodidae. (2) The vas deferens is far more highly differentiated than in *Nautilus* (Griffin (1900, Pl. X, fig. 38)). As far as concerns the absence of the coecum, and the smallness of the prostate and Needham's organ, which Ebersbach considers a simplification of the Octopod type, it has to be admitted that in default of embryological knowledge we have no criterion as to whether the absence or small size of an organ is an indication of a vestigial or rudimentary condition. No one, for example, would claim that the relatively small Needham's organ in *Nautilus* is necessarily vestigial. In making the foregoing criticism of Ebersbach's case I do not wish to assert that the male system in the Cirrata is necessarily archaic. All I wish to suggest is that it is by no means certain that its simplification is secondary.

*Special Glands.*—The " White Body." In *Chunioteuthis* and *Opisthoteuthis* the white body is of normal size. In *C. umbellata* it is " stark reduziert " (Ebersbach, *l.c.*, p. 398) and also in *Cirrothauma* (Chun, 1914, fig. 10). According to Faussek (1903) this structure is an organ for the elaboration of leucocytes.

2. *Branchial Heart.*—This organ, which is excretory in function, appears to have the same histological structure as in the Octopodidae and otherwise to show no important deviations. As far as I could find (Robson, 1926*a*, p. 1343) there is no important difference in size.

3. *Appendage of the Branchial Heart.*— The function of these organs, which are homologous with the pericardial glands of other Mollusca, is obscure. Grobben and Meyer (*l.c.*, p. 229) think it assists in the excretory function of the branchial heart. In *Opisthoteuthis* its structure seems to resemble that of *O. defilippi*. In the forms investigated by Ebersbach the structure seems to resemble that of various Octopodidae.

4. *Branchial Glands.*—The function of these organs is unknown. The structure and position does not seem in any way different from those of other Dibranchiata. From the admittedly scanty data given (Robson, *l.c.*, p. 1345) I concluded that there is a tendency for these structures to be smaller in the Cirrate and other abyssal Octopoda.

*Skeletal Structures.*—(a) *Cephalic cartilages.* In the Dibranchia there is usually a tough and strong cartilaginous capsule, which acts as a covering for the circumoesophageal nerve-mass. In *Opisthoteuthis* this seems to be normal. Ebersbach's remarks on the form with which he worked seem (*l.c.*, p. 374) to suggest that the normal cartilaginous substance is modified in *G. umbellata* by its transformation into a "Bindegewebslamelle," which "ist an manchen Stelle nicht mehr nachweisbar." In *Chunioteuthis* the cartilaginous investment of the statocysts are well developed.

(b) *Shell-vestige.*—("Flossenstütze," "Fin Supports," "Dorsal Cartilage.") Within the tissues of the dorsal part of the apical region of the body is to be found the solid body variously known as the Fin Support or Cartilage, Shell Rudiment, etc. This has three principal forms: (1) a more or less saddle-like plate, (2) a half-hoop or horseshoe-like structure, and (3) a widely V-shaped bent rod which may become more or less straight. The first form occurs in *C. mülleri*, the second in *G. umbellata*, and the third in *Chunioteuthis* (broadly V-like) and *Opisthoteuthis* (rod-like). As all the evidence as to the shell-rudiment in the Vampyromorpha points to it being a flat and rather broad or oblong plate, I think the form found in *C. mülleri* is more primitive than (2) and (3) (above) and the two separate "lateral stylets" found in *Octopus*. The latter may be reasonably derived from the cirromorph structure by the separation of the two limbs of the V-like organ in *Chunioteuthis*. It should be noted that Verrill (1883, p. 114) records that the fin-supports of *Opisthoteuthis agassizii* "are not united across the back as they appear to be in both the related genera." Actually he did not figure this structure and only alludes to it briefly. If this account is accurate it may represent an intermediate condition between the Cirrata and Octopodidae. The Cirrate type is thus to be considered as more archaic than the stylets of *Octopus*. As regards the origin and nature of this structure I do not think there can be any ground for suspecting that it is anything other than the vestige of the shell. H. Müller (in Meyer, *l.c.*) was the first to draw attention to the similarity in place of origin and mode of formation of the stylets of *Octopus* to the Decapod shell-vestige. Appellöf (1899) investigated the subject thoroughly in several of the Octopodidae and described the vestige, which is composed of a chitinous or chitin-like substance, and derived from an undoubted shell-sac. The more elaborate structure in the Cirrata has been studied by Meyer (*l.c.*), Ebersbach (*l.c.*) and myself (MS.), and the histological structure may be said to resemble in its essentials that described by Appellöf (but see p. 17). Ebersbach noted that the isolated, deeply-staining nuclei observed in *Octopus* and *Opisthoteuthis* are not found in *Chunioteuthis* and *G. umbellata*. A further indication of the homology of the Octopod "Schalereste" with the Decapod shell is the fact that in the Cirrata (as in the Octopodidae) the depressor infundibuli muscles are inserted into the "Flossenstütze" (Ebersbach, *l.c.*, p. 378), just as in *Sepia* they arise from the shell (Pelseneer, 1906, p. 291). It is only necessary to recall the fact that in a Decapod like *Sepia*, the shell arises in the embryo from the shell-sac, the outer layer of which secretes a plate of conchyolin in which the mineral substance is subsequently laid down. The Octopod shell-vestige is no doubt homologous with this

plate. It must be finally understood that by the word "shell-vestige" we do not imply a homology with the true shell (ostracum), but with a portion of the secondary shell.

(b) *Systematic.*

Family 1. CIRROTEUTHIDAE, Keferstein. The mantle-aperture is rather narrow; but not closed round the base of the funnel. A crop is present. The gills are "sepioid" and there is no median adductor. The shell-vestige is saddle-like. There is a "secondary" web. The body is elongate and the head is prominent. Probably archaic.

Genus **Cirroteuthis,** Eschricht, 1838.

With the characters of the family.

*Type of the genus.*—*C. mülleri,* Eschricht.

**Cirroteuthis mülleri,** Eschricht.

(Text-fig. 18.)

*Cirroteuthis Mülleri,* Eschricht (1838, p. 633, Pls. XLVI–XLVIII).
*Sciadephorus Mülleri,* Prosch and Reinhardt (1846, p. 187, Pls. I–V).
*Cirroteuthis Muelleri,* Mörch (1877, p. 440).
,, *mülleri,* Hoyle (1886, p. 60).
,, *Mülleri,* Lönnberg (1891, p. 6).
,, ,, Appellöf (1893, p. 1).
,, ,, Posselt (1899, p. 269).
,, ,, Appellöf (1899, Pl. 1, figs. 6–7).
,, *mülleri,* Friele and Grieg (1901, p. 123).
,, ,, Pfeffer (1908, p. 23, fig. 13).
,, ,, Robson (1926*a*, *passim*).

*Holotype.*—In collection of the Naturhistorische Verein of Breslau and Bonn (cf. Eschricht, *l.c.*, p. 627).

*Specimen seen.*—One from the "North Sea" (?). ("Purchased of Prof. Steenstrup.") Brit. Mus.

*Distribution.*—Jakobshavn, Greenland (Eschricht, Prosch and Reinhardt, etc.); "Greenland Coast" (Lönnberg); Stn. 297, Norwegian N. Atlantic Expedn. (72° 36′ N., 5° 12′ E., N.E. of Jan Mayen), in 1280 fms. (Appellöf, Friele and Grieg (the latter add "also found during the second North Atlantic Expedition in 1900"—where?)); "North Sea" (Brit. Mus.).

*Description.*—The body is elongate and oblong. In the British Museum specimen the interocular width is 43% of the mantle-length; in Eschricht's specimen it was about 45%. The eyes are small. In the British Museum specimen the diameter is only 13 mm. The body behind the fins is about as wide as the head in the British Museum specimen, rather broader in the type and that figured by Reinhardt and Prosch. The body itself is about one-third of the total length. The arms in the type have the formula 2 = 3, 1 = 4. They are about 66% of the total length. The suckers are very small (about 2·5% of the body-length). There are about 30 suckers on each arm, of which 25–27 are conterminous with the web. There is one very remarkable feature in the British Museum

specimen which is noted neither by Eschricht nor Prosch and Reinhardt. On each arm, beginning in the same place, viz. after the 7th in the series, the suckers lose their cup or bowl-like character and become quite flat. The normal structure gradually reappears and is found complete at about the 21st sucker. This remarkable modification is quite regular; but it is not impossible that it may have been produced by some accidental pressure on the suckers. The cirri are very long (12–18 mm. Brit. Mus.), and five to seven times as long as the diameter of the suckers. They begin between the second and third suckers, and are continued to the edge of the web. The latter is very extensive. It does not extend right to the tips of the arms, of which a few millimetres are free. But, as Eschricht pointed out, the length of a radius drawn midway between adjacent arms is longer than the arms, as the edge of the web is markedly convex. One such radius in sector C of the left side measures at least 12 mm. more than the adjoining arms (Brit. Mus.). The tips of the arms are so fixed to the web that they all point dorsally, being attached to the web on their dorsal edge for a longer distance than on the ventral side. This was noted by Eschricht (*l.c.*, p. 630). The arms are attached to the web by a shallow intermediate web measuring 20–17 mm. at the most. The fins are considerably wider than the head, viz. nearly twice (Brit. Mus.), over $1\frac{1}{2}$ times (Reinhardt and Prosch) or $1\frac{1}{3}$ times (Eschricht). Their width is rather more than half the length. The fins are inserted into the body close to the eyes in Eschricht's figure (Pl. XLVII) and similarly in Prosch and Reinhardt's Plate I (but not in Plate V). In the British Museum specimen they are placed half-way between the eyes and apex, the whole body being far more like that of *S. syrtensis*, Verrill. The edges are more or less parallel, and the line of insertion is about as wide as the fins themselves in the type and British Museum specimen. In Prosch and Reinhardt's figure (Pl. V) they are flabellate, and the sides are not parallel. The dorsal cartilage has been figured by Prosch and Reinhardt (Pl. III, figs. 1–3) and Appellöf (1899, Pl. I, figs. 6–7). I will figure that of the British Museum specimen later (1932), as there is plainly some variation in this structure; neither of the two other figures is very clear. The cartilage is saddle-like, with a deep indentation at one end. The general colour of the type seems to have been a very pale (probably hyaline) brownish mauve, which may have been deeper on the oral surface of the web. The arms and viscera seem to stand out against the pale colour. The mantle-aperture in Eschricht's figure (Pl. XLVIII) is widely open. The actual amount of "gape" is difficult to assess; but it looks at least like stage B (Robson, 1926*a*, p. 1334). This is what I find in the British Museum specimen; though in Prosch and Reinhardt's figure (Pl. V) it is narrower. The funnel is long and tubular with a broad base. I could find no trace of either the funnel-organ or a valve. The gills are not very well preserved. It is clear, however, that they are of the less specialized type (cf. Prosch and Reinhardt, Pl. IV, figs. 1–2), *i.e.* not of the "half-orange" type found in other Cirromorpha (p. 124). Prosch and Reinhardt seem to show 8–9 filaments a side. I could certainly count 8. The mandibles are figured by Prosch and Reinhardt (*l.c.*, fig. 6 (1–4)). Only the lower mandible of the British Museum example is available. It resembles that figured by Prosch and Reinhardt, and is very characteristic in (1) its

short gular lamella, (2) thick rami and great width. The beak is sharp and there is no subrostral prominence. In the upper jaw the rostral lamella is very large, being as deep as the palatine. I could find no trace of a radula. The anterior salivary glands are very small; the posterior absent. There is a very moderate crop-like enlargement of the oesophagus. The stomach is large, thick-walled, and has a strong, dense cuticular lining. The coecum is large but not spiral. The intestine is short, very stout, and shows some trace of a proximal enlargement (" third stomach "?). There is no ink-sac. I dissected the genitalia of the British Museum specimen, a male. They are rather macerated, and I am not at all certain of the details. On the whole they seem to combine features of *Chunioteuthis* and *Grimpoteuthis wülkeri*. There is no accessory gland and (?) no third seminal vesicle. Needham's organ seems to be represented by an adherent vesicle. No spermatophores were found. In Prosch and Reinhardt's figure (*l.c.*, fig. 5) the seminal vesicles are not shown. The female organs are figured by Prosch and Reinhardt (*l.c.*, fig. 3). They are unilateral, and the vagina is very short and subcircular. The spermoviducal gland is very large and the oviduct thick and of moderate length. The ovarian eggs attain a large size.

*Nervous System.*—This was figured by Prosch and Reinhardt (*l.c.*, Pl. V, fig. 2). It seems to be compact, and the constituent ganglia are apparently as much fused as in *Grimpoteuthis*. There is (*e.g.*) no separate brachial ganglion. The stellate ganglion is situated as in the Decapoda (see p. 126). What appears to be a large peduncular ganglion is figured on the optic nerve (? ganglieformede Kjertler).

*Remarks.*—This is a clearly characterized form. It is possible that Verrill's *syrtensis* may be a variety (see p. 135). Though taken on several occasions in the last century, it has only been taken once or twice since Mörch's notice of it, unless some of Posselt's records (*l.c.*) indicate more recent captures. At present it is only known from W. Greenland and the N. Atlantic N.E. of Jan Mayen. The British Museum specimen was obtained in " the North Sea "; unfortunately no more data are given.

The generic position of the various species which have been placed in *Cirroteuthis* or *Stauroteuthis* is by no means easy to distinguish. The general tendency has been to divide them into two genera, *Cirroteuthis* and *Stauroteuthis*. Grimpe (1916, p. 355), who actually recognized two subfamilies (Cirroteuthinae and Stauroteuthinae), defined them according to the character of the fin-support. The former had the sup port " saddle-like without limbs " (Schenkel), the latter had them " horseshoe-like with forwardly pointing limbs." One other diagnostic feature was mentioned. Berry (1912*a*, p. 274) distinguished *Stauroteuthis* from *Cirroteuthis* " chiefly in the fact that the dorsal cartilage is posterior in position and horseshoe-shaped, with the free ends directed towards the head." In 1920, however, Joubin (1920, pp. 14, 21) objected to the distinction, and a few years later I discussed the matter at some length (Robson, 1924*a*, p. 676). I pointed out that among the forms placed in the two genera in question there were so many different forms of support that a single division into saddle-like and horseshoe-like was inadequate. However, neither I nor any of my predecessors were able to make a synthetic study of all the available characters with a view to

finding out if there were any clearly marked associations. I discussed (*l.c.*) this question as far as I could, but concluded that " so few forms have crystallized out into these combinations or any satisfactory generic character-complexes " that it was necessary to await more information.

My present opinion, after having had an opportunity of examining the question more thoroughly, is rather half-way between the Berry–Grimpe view and that of Joubin–Robson. In short, I believe that certain marked divergences are seen in the group and that, when we contrast *Cirroteuthis mülleri* (*e.g.*) with *Grimpoteuthis glacialis*, these appear of major importance. When, however, we come to decide what forms are to go with *mülleri* into *Cirroteuthis* and what with *glacialis* into *Grimpoteuthis* it is by no means so easy to distinguish simple easily contrasted assemblages, because there are so many forms that combine the characters of the extremes and show distinctive tendencies of their own as well.

The subject may be most readily explained as follows. *C. mülleri* and *C. magna* agree very closely in having a saddle-like shell-vestige, which puts them at once in a different category from those having a V-shaped vestige. They also have the peculiar feature known as an " intermediate web. " They agree in sundry minor details (long cirri and fins) and differ in gill-form and the length of the body. On the whole, they may safely be treated as congeneric. My *C. hoylei* should almost certainly be associated with them, though it is in a very fragmentary condition. Now one other species possesses the saddle-shaped vestige (*Cirroteuthopsis massyae*), but the web is normal and the suckers and fins are small. On the shell-vestige it should rank as a *Cirroteuthis*; but it is otherwise *Stauroteuthis*-like. *Stauroteuthis syrtensis* is another difficult case. It has a V-shaped vestige, but Verrill's figure (1882, Pl. XXXII, fig. 1) shows an intermediate web, and the text most plainly indicates the same structure (*l.c.*, p. 383). Furthermore, the shape of the body is remarkably like that of *C. mülleri*.

An intermediate web is found in *Chunioteuthis ebersbachii* (Grimpe, (1916, p. 356), " Zwischensepta vorhanden ") associated with a broadly V-shaped support, and the same association occurs in *C. gilchristi*. *Ebersbachii* and *gilchristi* have in addition the unique characteristic of having the pallial aperture and funnel confluent. One of Verrill's specimens of *S. syrtensis* (see p. 136) seems also to show this condition.

In none of the remaining species can I find evidence of an intermediate web, and all have a U- or V-shaped support. There is, however, a good deal of divergence in the form of the latter.

I do not think any of the other characters can be made use of in generic divisions. It is likely that some of the characters of the genitalia might be thus serviceable, but they are very imperfectly known.

We are plainly faced with a tiresome difficulty with regard to *syrtensis*, *massyae*, *ebersbachii*, etc. What it amounts to is this, that the extreme forms of our series (e.g. *mülleri* and *glacialis*) are very clearly distinguished and should be treated as representative of different families. But we have a number of forms which are intermediate and can only be given generic names on quite arbitrary grounds. The generic diagnoses given below probably represent natural divergences, but are we to treat *syrtensis* as a " *Stauroteuthis* " because its support is V-shaped or a *Cirroteuthis* because it has an intermediate web? The same question *mutatis mutandis*

may be asked of *C. massyae*. The following tabulation indicates the affinities of *syrtensis*.

Long body = *Cirroteuthis*, Eschr.
General shape ,,
Intermediate web ,,
Absence of a septum ,,
Long cirri ,,
Shell-vestige V-like = *Stauroteuthis*, Auctt.
Gills? of "half-orange" type ,,

It is thus seen that it is on the whole nearer akin to *Cirroteuthis* than to, e.g., *umbellata* or *glacialis*, though it probably has two characters in common with the latter. In view of this uncertainty it seems better to retain it in its original genus and create a new one for *umbellata*, etc. The genera thus distinguished are as follows.

*Cirroteuthidae.*

1. *Cirroteuthis*: Fin-support saddle-like; an intermediate web present. The cirri tend to be much longer than the diameter of the suckers. The fins are usually longer than the head is wide.

   *C. mülleri.*

   *Stauroteuthidae.*

2. *Stauroteuthis*: an intermediate web present; shell-vestige V-like; fins small; cirri large; body long (= *C. mülleri*); fins median; no median septum.

   *Stauroteuthis syrtensis.*

3. *Grimpoteuthis*, n. gen. (olim *Stauroteuthis*, Auctt.): the fin-support V- or U-like; no intermediate web; the cirri usually little larger than the diameter of the suckers (× 3 at most); the fins usually less than the head-width.

   *G. pacifica, meangensis, plena, umbellata, caudani, hippocrepium, megaptera, albatrossi, grimaldii, mawsoni, wülkeri*, sp. A, sp. B, *glacialis.*

4. *Chunioteuthis*: the fin-support widely V-like; an intermediate web present; pallial aperture and funnel confluent; fins small; cirri large; body small; fins terminal.

   *Ch. ebersbachii, gilchristi.*

Incertae sedis: *Cirroteuthis magna, hoylei, Cirroteuthopsis massyae.*

I do not think it is desirable at present to recognize any subfamilies within the Stauroteuthidae.

Family 2. STAUROTEUTHIDAE, fam. nov. The web is usually simple. The mantle-aperture is either reduced to a narrow slit closely fitting round the base of the funnel or confluent with the orifice of the latter. The median adductor is usually present. The gills are of the "half-orange type." The shell-vestige is U- or V-shaped.

Genus 1. **Stauroteuthis,** Verrill, 1879.

For definition see above.

*Type of the genus.*—*S. syrtensis,* Verrill.

**Stauroteuthis syrtensis,** Verrill.

*Stauroteuthis syrtensis,* Verrill (1879, p. 468).
„ „ *id.* (1880*a*, p. 294, Pl. XVI, figs. 1–5).
„ „ *id.* (1882, p. 382, Pl. XXXII, figs. 1–5).
„ „ *id.* (1884, p. 249).
„ „ *id.* (1885, p. 409).
„ „ *id.* pars ? = *Chunioteuthis ebersbachii,* Grimpe (1916, p. 351).
*Cirroteuthis syrtensis,* Robson (1926*a*, p. 1328).

*Holotype.*—In U.S. Nat. Mus.

*Distribution.*—Banquereau, E. of Sable Island in 250 fms. (Verrill, 1879); "Albatross," Stn. 2034, in 1346 fms. (*id.*, 1884); 39° 25′ N., 71° 49′ W., in 523 fms. (*id.*, 1885, p. 409).

*Description.*—Verrill gives :—length from end of body to base of arms, 160 mm. and length of arms, 330 mm. In his figure, however, the body to the base of the arms is about half the total length (*i.e.* as long as the arms) ! Perhaps we should read "length to tip of arms" instead of "length of arms" ? The body is narrow and ovoid-oblong and resembles that of *C. mülleri.* The width across the eyes is about 27% of the body-length. The body is 45% (or 32%, see above) of the total length. Apically it is distinctly narrower than in front of the fins. The arms are slender and subequal. They are 68% or 55% of the total length. They each bear 55 or more suckers. The size of these is not given. In the middle of the arm they are 12 mm. or more apart. The cirrhi are intercotyledonary and are very long (25–32 mm.). They commence at the 5–6th suckers on the dorsal arms and between the 7th and 8th on the rest. They are not continued to the extremities, ceasing at the 23rd sucker on the dorsal and lateral arms and at the 22nd on the ventral ones. "Near the mouth and beyond the last cirri on the free portion of the arms, the suckers are more closely arranged." The eyes are said to be large; but judging by their area (from the figure) they individually occupy only a fractional part of the mantle-area. There is a deep intermediate web (38 mm. at its greatest depth). The fins measure 33 × 44 mm. and are relatively small, though they are about as long as the interocular width (according to Verrill's measurements; the actual figure shows them as less). They are widest at the base, rather pointed, and occupy a median position on the body. The periphery of the body beyond the fins is edged by a thin membrane about 12 mm. wide. The colour (in alcohol) is "pale with irregular mottlings and streaks of dull brownish; inner surface of arms and web towards the base, and membrane around the mouth, deep purplish brown." The funnel is slender and elongate and projects some distance from the very narrow pallial aperture which closely embraces its base. There is a V-shaped dorsal cartilage. (The "internal cartilages" of the fins mentioned by Verrill must surely be the pad of elastic tissue (p. 119).) The jaws are small, but of normal form. The beak of the dorsal mandible is about half as deep as the palatal

lamella. The septum is absent (?). The gills, from Verrill's brief description, seem to be of the *Opisthoteuthis*-type and to consist of 10–8 lamellae apiece. The oviduct is single and the vaginal aperture nearly median. Verrill describes a large nidamental gland (? spermoviducal gland) "consisting of a posterior yellowish portion and a much larger round dark brown anterior portion." The "portion behind these glands" [? oviduct] is thin and tubular. The vagina is large and thick. The eggs in the vagina are provided with a hard reddish-brown case. "Seen endwise" the eggs have "a broad elliptical outline and, while the two ends are truncated and smoothish, the sides are ornamented with numerous regular, roughened, elevated ribs." Greatest breadth of the egg 11 mm.; lesser breadth 7 mm.; length 6 mm. The young specimen from Stn. 2034 briefly mentioned by Verrill (1884, p. 249) has the bodily proportions of the adult (head and body 11 mm., total length 21 mm.). The fin is, however, much larger than in the type (length 9 mm., depth 3 mm.). The web is nearly as deep as the arms are long. It is impossible to criticize Verrill's diagnosis. His third specimen is of a rather different form. Its width is about 70% of the length, and the body is 16% of the total length. The fins are 12 mm. long and are slightly less than the interocular width. The web is 69% of the arms. The cirri are half ($\frac{1}{2}\frac{0}{0}$) as long as the visceral sac, in the type they are $\frac{3}{1}\frac{2}{4}\frac{}{0}$* *i.e.* about a quarter of the length. The pallial aperture is a small circular pore from which the siphon does not protrude.

*Remarks.*—Apart from the uncertainty as to the measurements in which the arms are involved, this form seems very characteristic. The long, narrow body and small eyes (? covered by the integument) and fins combine to render it unlike any other form. It is quite impossible to say if Verrill's two young specimens were correctly diagnosed. The fins are inordinately large in the smaller, which may be a young *Grimpoteuthis megaptera*, and the body is short in the other. In the latter, moreover, the funnel is not exserted. Verrill thinks this may have been accidental, but I am inclined to agree with Grimpe (*l.c.*) that the condition is like that in *Ch. ebersbachii*. Whether Verrill's form should be placed in Grimpe's genus on this account alone is a little uncertain, but I am inclined to accept Grimpe's view.

Genus 2. **Grimpoteuthis,** new genus ("*Stauroteuthis*," Auctt., "*Cirroteuthis*," Auctt.).

The shell-vestige is V- or U-like. There is no intermediate web. The cirri are usually little longer than the diameter of the largest suckers. The gills are of the "half-orange" type. The fins are usually shorter than the width of the head.

*Type of the genus* :—*G. umbellata* (Fischer). See remarks on p. 139.

* Length of body taken as 160–20 mm.

**Grimpoteuthis umbellata** (Fischer).

(Plate II, fig. 1, text-figs. 19–20.)

*Cirroteuthis umbellata*, Fischer (1883, p. 404).
,, ,, Joubin (1900, p. 21, Pls. I, III and XII, text-fig. 1).
,, ,, Fischer and Joubin (1907, p. 318, Pls. XXIII and XXV, text-fig. 1).
(*not*) ,, ,, Massy (1909, p. 4 = *Cirroteuthopsis massyae*, Grimpe).
,, ,, Chun (1914, p. 21, pars).
,, ,, Ebersbach (1915, *passim*, pars).
,, ,, Joubin (1920, p. 13).
,, ,, Grimpe (1920*a*, p. 230 and foll.).
,, ,, Joubin (1924, p. 9).
,, ,, Robson (1926*a*, *passim*).

*Syntypes.*—Not traced.

*Specimens seen.*—(*a*) In Mus. Oc., Monaco, 4 specimens (Stns. 753, 2994, 2986 and 3412). (*b*) Bergen Museum, 2 specimens ("M. Sars," Stn. 53).

*Distribution.*—Arguin Bank, W. Africa (23° 50′–52′ N., 19° 37′ W.), in 623–683 fms. (grey mud) [Fischer, *l.c.*, p. 404, who also gives "entre Cap Noun et les Canaries, 1235 m."] (Fischer, Joubin and Fischer); off Azores (39° 54′ N., 20° 27′ W.) in 2388 fms. (white mud and Globigerina ooze) (Joubin); off the Azores (37° 55′ N., 29° 22′ W.), in 1222 fms. (Fischer); Gulf of Gascony (45° 07′ N., 7° 06′ W.), in 2664 fms. (Globigerina ooze); 44° 8′ N., 10° 44′ W. in 2735 fms.; Sigsbee's Deep (39° 59′ N., 56° 20′ W.), in 2882 fms. (Joubin); (34° 59′ N., 33° 1′ W.), in 1430 fms. (Chun).

*Description.*—This seems to be a very variable form and I am not certain that more than one species may not have been described and recorded under the name. See Remarks (p. 139).

(a) *Adult.*—None of the specimens taken are particularly large. One of Joubin's specimens (1920) measures 235 mm. over all. The body is usually about a third of the total length, and is therefore large for a Cirromorph. It is distinctly less in one of the "M. Sars" specimens, viz. 23%. It is about as wide as long or less (100–62% ("M. Sars")), and the interocular index is about the same as the body-width or it may exceed it. The arms are usually in the order 1.2.3.4 and are (?) 77–66% of the total length. The suckers are very small, scarcely exceeding 3·0% of the body-length. The cirri are continued to the extremity of the arm (cf. Joubin, 1920, p. 14). They are very small, and from the figure on one of Joubin and Fischer's plates they are at the most not more than two or three times the diameter of the suckers and often are scarcely as wide as the latter (? contracted). The web seems to be in the order ABCDE, but cf. Joubin and Fischer (1907, fig. 1).* Joubin's figures for length give us a very high index of 67, with E very much smaller than A (under half). Neither the figure published in 1900 nor that in 1907 indicates such a marked difference. The range of length in the web is 67–50%. The fins are very variable in shape and size. They are usually median in position and their width is about two-thirds of their length. The other varies from about $\frac{3}{5}$ of the interocular width (Joubin, 1900)

* On the ventral side of the arms the web terminates abruptly in a "tubercle" (see p. 143).

to almost $1\frac{1}{2}$ that dimension (" M. Sars "). The colour of the 1900 specimen was brick-red, becoming a deeper violet shade towards the web. The oral surface of the web is " d'un beau violet velouté, foncé." The tissues are very gelatinous and are semi-transparent. The pallial aperture is not described, but from Joubin and Fischer's figure of the funnel (1907, Pl. XXIII, fig. 5) it would seem to be more or less free of the latter. The funnel is long and narrow. Its lateral pouches are rudimentary and the longitudinal siphonal muscle-pillars are likewise very poorly developed. The median adductor is very imperfectly developed (Ebersbach). The gills have been well described by Joubin and Ebersbach,* who were the first to note the curious change in orientation of the gill in these animals. They are of the " *Opisthoteuthis* " type, and have 7–8 filaments. The branchial gland is present. The branchial heart and

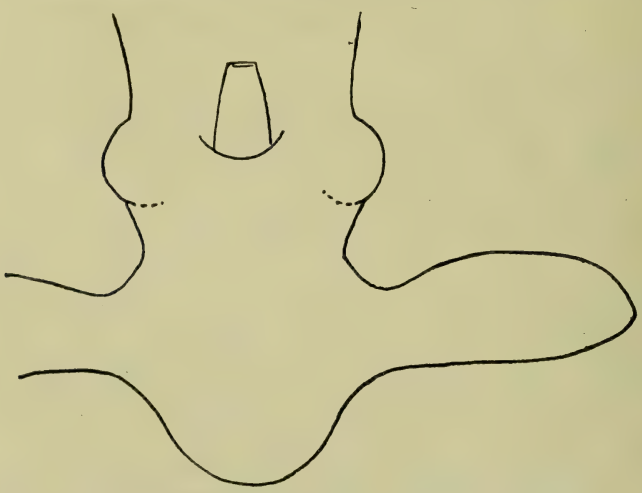


Fig. 19.—*Grimpoteuthis umbellata* (?). (Mus. Océanogr., Monaco.) Stn. 2986 (1910).

the sac of the kidney are " peu developpés." The other important organs are described by Ebersbach. Joubin (1900, p. 24) seems to suggest that he noticed spermatophores, but this point is obscure. The dorsal cartilage according to Joubin (1920, p. 14) is horseshoe-shaped. It was not figured by him, and I do not know if in all his specimens it agrees with that figured by Ebersbach (*l.c.*, text-fig. 7), which is hoop-like with the arms turned outwards somewhat. This agrees fairly well with that of a specimen from Stn. 2994 (Monaco), less clearly with the one from Stn. 2986, which is shorter and broader.

(b) *Juvenile.*—Fischer and Joubin (1907, Pl. XXV, figs. 9–10) figure a small specimen which they assign to this species without much hesitation. It is about 25 mm. over all. The body is a third of the total

* I do not follow Ebersbach, who says of the gill that it has a great resemblance to that of *Opisthoteuthis* (p. 124). He mentions an *Octopus*-like " zweireihige Anordnung " of the filaments, and his figure (p. 396) shows this condition. There is here a very marked divergence between the gills of Joubin's specimens and the two smaller " M. Sars " specimens on the one hand, and the larger " M. Sars " example, which Ebersbach described, on the other.

length and as wide as it is long. The head is as wide as the body. The fins are relatively longer than in the adult and about as long as the body is wide. They seem to have parallel sides and to be directed anteriorly. Unlike the undetermined species A (p. 155), which it rather resembles, the fins are median, not terminal. The funnel is long and prominent, the pallial aperture narrow. The animal was a bright rose colour without any trace of violet pigment on the web.

*Remarks.*—In 1914 Chun reported a number of specimens of a Cirroteuthid which he called *C. umbellata* from Stations 25, 53 and 70 of the "Michael Sars" Expedition. These were anatomically examined and described by Ebersbach (1915) and Grimpe (1916, 1920). Unfortunately Ebersbach, who distinguished representatives of two distinct genera among Chun's specimens, did not sufficiently define to which of the "Michael Sars" specimens his anatomical descriptions applied. Grimpe, however, defined this with precision. The identity is, nevertheless, by no means clear, and, as a result, I fell into the error (1926*a*) of ascribing to Grimpe's *Stauroteuthis wülkeri*, which is founded on the "Michael Sars" specimen from Station 25, the anatomical description of "*C. umbellata*" given by Ebersbach. For this reason I have thought it best to clear up the identity of the various specimens by means of the following table. I am indebted to Professor Grimpe, who worked with the late Dr. Ebersbach, for clarifying this situation.

| Chun (1914). | Ebersbach (1915). | | Grimpe (1916, 1920). |
|---|---|---|---|
| Stn. 25, example 1 | not dissected | | *Stauroteuthis wülkeri* (1920) |
| „ 53 „ 1♂ (largest) | dissected | "*Cirroteuthis umbellata*," Ebersbach | see below |
| „ 2♀ | partly dissected (not included in description) | | |
| „ 3 | not dissected | | |
| „ 4 | „ „ | | |
| „ 70 „ 1 | dissected | = "*Stauroteuthis*, sp." | *Chunioteuthis ebersbachii* (1916) |

Of the four specimens from Stn. 53 Grimpe says (1920*a*, p. 234), "das grösste der ersteren wurde von Ebersbach anatomisch genau untersucht. Der Rest befindet sich augenblicklich in meiner Hand. . . . Es ist mir dabei aufgefallen dass sich zwar die 3 von Statn. 53 noch vorhandenen Stücke untereinander völlig gleichen und auch mit den früheren Beschreibungen (Joubins, P. & H. Fischers . . . [as *umbellata*] gut übereinstimmen." It therefore follows that of the six "Michael Sars" specimens, one (Stn. 70) = *Ch. ebersbachii*, Grimpe (= *Stauroteuthis* sp., Ebersbach), a second (Stn. 25) = *Stauroteuthis wülkeri*, Grimpe, and four (described as "*umbellata*" by Ebersbach) are referable (*fide* Grimpe) to that species. I ought to draw attention to the fact that the specimen figured by Ebersbach (text-fig. 1) as *C. umbellata* is that subsequently described as *S. wülkeri*, and that the anatomical data given by Ebersbach do not apply to it.

By kind permission of the Director of the Bergen Museum I have received from Prof. Grimpe two of the "Michael Sars" "*umbellata*," and

I am now able to add the following information concerning them. They show at least three notable divergences from the other known specimens of *umbellata*, viz. (1) that the body is much smaller and the arms longer, (2) that the fins are longer and on the whole narrower, and (3) the general shape of the visceral mass and the disposition of the fins differ markedly at least from that figured by Joubin (1900). There is agreement in the residual characters, but it will be seen that our data by no means indicate a homogeneous array, and for the time being I am somewhat doubtful as to the correct identification of all the specimens named *umbellata*. As to the identity of the "Michael Sars" specimens, I am somewhat unwilling to regard them as conspecific with that figured as *umbellata* by Joubin (1900, Pl. 1), though I freely admit that the other specimens of *umbellata* serve to bridge the gap. Certainly the fins and shape of the body of the "Michael Sars" specimens are not unlike those of *megaptera* as figured by Joubin (1920, Pl. 1), though not those

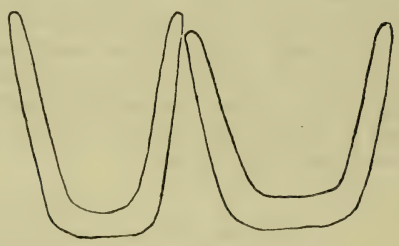



Fig. 20.—*Grimpoteuthis umbellata* (?). Shell-vestiges. (Mus. Océanogr., Monaco.) (*a*) Stn. 2994 (1910); (*b*) Stn. 2986 (1910).

in the type-description. It may well be that Joubin's *megaptera* is an extreme form of *umbellata*. However, it seems better for the time being to treat the "Michael Sars" specimen as referable to *umbellata*. Another point to note is that the "Michael Sars" specimens and Joubin's all have six filaments in the gill, and the median pallial adductor is very small. Joubin (1920, p. 15) compares Hoyle's *Stauroteuthis hippocrepium* with this species. It is unfortunate that Hoyle's description was so meagre, as there is sufficient similarity between the Pacific and Atlantic species to make the comparison plausible. I do not think, however, it is a matter that can be profitably discussed. It is rather a pity that all the known specimens are not fully described. It is desirable to know, *e.g.*, if the Sigsbee's Deep specimen and the E. Atlantic forms are really synonymous.

### **Grimpoteuthis megaptera** (Verrill).

(Text-fig. 21.)

*Cirrhoteuthis megaptera*, Verrill (1885, pp. 405, 446, Pl. XLIII, figs. 1–2).

? *Cirroteuthis Richardi*, Joubin (1903, p. 101).

*Cirroteuthis megaptera*, *id.* (1920, p. 15, Pl. I, figs. 1–4).

„ „ Robson (1926*a*, *passim*).

*Holotype* (?).—In U.S. Nat. Mus.

*Specimen seen.*—One from Stn. 1150 (M.O., Monaco).

*Distribution.*—" Albatross," Stn. 2225 (36° 05′ N., 69° 51′ W.), in 2512 fms., on yellow ooze, temp. 37° F.; Stn. 2224 (36° 16′ N., 68° 21′ W.), in 2574 fms., on Globigerina ooze; Stn. 2220 (39° 43′ N., 69° 23′ W.), in 1054 fms. (Verrill); 16° 12′ N., 24° 43′ W., in 2128 fms. on sandy mud (volcanic), Chalut (Joubin).

*Description.*—The following description is based on that given by Verrill with sundry additions from Joubin's data. The latter did not, however, give a full description and very few measurements. The body is described as " very short." * The head is large and broad, its width being about 83% of the body-length (fig.). The eyes are small, their individual area (9 × 9 mm.) being $\frac{1}{12}$ of the mantle area (37 × 27). The arms are in the order 1.2.3.4 and are 88% of the total length in the type. The suckers are very small. At the middle of the arm the intervals between the suckers is often double their diameter. The cirri are described by Verrill as small and alternating. In Joubin's figure (Pl. 1, fig. 4) they seem to be about three times the diameter of the suckers.

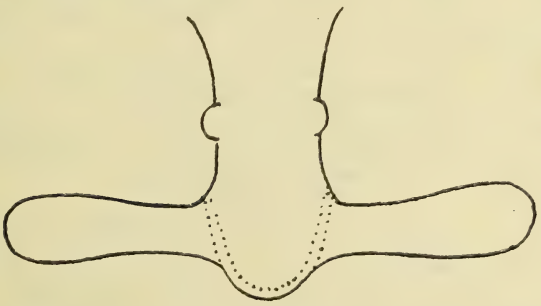


Fig. 21.—*Grimpoteuthis megaptera.* (From a sketch of a specimen (Stn. 1150) in Mus. Océanogr., Monaco.)

Their distribution is unknown. The fins in Verrill's two larger specimens are 33 × 11 and 24 × 9 mm. In the smaller they are 9 × 4·5. In the figure (Pl. XLIII) they easily exceed the interocular width. In the description of one of the larger specimens they are just under that width (27 : 24). In the two larger specimens the width of the fins is calculated as about $\frac{1}{3}$ the length, yet in the figure they are plainly wider (nearly $\frac{2}{3}$). In Verrill's drawing the posterior edge is nearly straight, the anterior very much curved, and the line of attachment is only half as long as the greatest width. *A propos*, however, of the shape of the fins, Verrill (*l.c.*, p. 406) says, " in the living state . . . the fins are much larger and broader, with the end more rounded; and the anterior edge is thinner and more convex than after preservation." If Joubin's specimen is correctly named (see below) this may account for the difference between the fins in his figures and in Verrill's. In Joubin's figure the width of the fins is a little more than half the length, the sides are almost parallel, and the line of attachment is nearly as wide as the maximum diameter. The fins are inserted rather nearer to the eyes than to the apex of the body. The web is thick and swollen. It has the formula AB = CD = E

* " Length of body to gill opening " (25 mm.) + 10 = apex-eye length (±).

and is 47% of the arm-length in the type. The colour of the body and fins is bluish white speckled and spotted with purplish brown. The arms and the outer and inner surface of the web are dark chocolate brown. The suckers are yellowish white with brown rims. The mantle-aperture is narrow, but not excessively so; the funnel projects freely and is broad and short. Verrill noted on the arms a " fleshy tentacle-like process at about the distal third of the arm on the posterior side near the edge of the web." . . . " When perfect, these organs, which are muscular, were probably united to the web and served to support or strengthen it." Joubin could find no such organs in his specimen. The dorsal cartilage is horseshoe-shaped ( ? exact shape) according to Joubin.

*Remarks.*—Verrill's description contains notes on five specimens. Four of these are much longer than the fifth. Of the former, one has much larger fins than the other one which is described. In one specimen from Station 2224 the body is much longer behind the fins than the others, and the web is but half the length of the arms. These features and the differences observed in Joubin's specimen might be considered evidence of specific diversity; but I think Verrill's warning as to the effect of preservation is reasonable, and for the time being I hold that these forms should be treated as conspecific.

**Grimpoteuthis pacifica** (Hoyle).

*Cirroteuthis pacifica*, Hoyle (1885, p. 235).
„ „ *id.* (1885*a*, p. 112).
„ „ *id.* (1886, p. 61, Pl. X).
„ „ (?) Goodrich (1896, p. 19).

*Holotype.*—In Brit. Mus.

*Specimen seen.*—One (the type) from off New Guinea.

*Distribution.*—" Challenger," Stn. 181 (13° 50′ S., 151° 49′ E.), off S.E. coast of New Guinea, in 2440 fms., on Red Clay.

*Description.*—The fragmentary specimen which Hoyle described as *pacifica* is in a very bad condition. I can do little more than reproduce Hoyle's description. The head was described as very short, and the eye seemed to have occupied " all the available space between the fin and the arms." The latter are in the order R. 1.4.2.3, L. 2.1.3.4. They are subequal, thick and taper rapidly towards the extremities. The suckers are 1·4% of the longest arms and little differentiated in size. There are about 52 on the longest arms. At the margin of the web they are rather closely crowded; half-way down the latter they are about a diameter or a little more apart. In section the basal cup is deep but thin walled. The cirri in such of the arms as are well preserved are not found immediately about the mouth. Hoyle states that on the dorsal arms they commence between the 7th and 8th suckers; on the ventral arms they start between the 6th and 7th. They are continued to the end of the arms. They attain their maximum length about half-way along. The longest are 5–6 mm. long or over twice as long as the diameter of the suckers. The web according to Hoyle's figure (? reconstructed) seems to have the formula BCADE. B may have been 58% of the arms. It seems to have been continued up the dorsal side of all the arms as a broad membrane reaching right to the tips, and to

have ended more or less abruptly on the ventral side. At the latter point of union is a tough nodule as in *Froekenia* and *G. umbellata*. Hoyle (*l.c.*, p. 62) says this had a cartilaginous consistency. On dissecting one I found that it was hollow and thick-walled. The plan of the web (but not the proportions of the sectors) is like that of *G. umbellata* (Joubin, 1907, p. 321). The fins measure 55 × 15 mm., and are thus long and narrow. They were " obovate " in shape. The extremity is broad and rather blunt, and the line of insertion is narrower by a third or more than the maximum width. The pallial aperture closely embraces the base of the long, thin and conical funnel. Of the other parts only the mandibles are known. The lower has a short and deep gular lamella and moderate beak; in the upper the beak is strong and the rostral lamella two-thirds as deep as the palatal. The colour was a " deep purplish madder, paler outside the umbrella and on the fin."

*Remarks.*—It is a pity no more details of this species are available. It seems to have been of the build of *G. megaptera*, but the funnel was much longer and the fins a different shape. The latter are not unlike those of *Grimpoteuthis* B (Robson, 1924*a*, p. 682).

### Grimpoteuthis meangensis (Hoyle).

(Plate I, fig. 1; text-figs. 22–23.)

*Cirroteuthis meangensis*, Hoyle (1885, p. 234).
,, ,, *id.* (1885*a*, p. 111).
,, ,, *id.* (1886, p. 63, Pl. IX, figs. 12, 13; Pl. XI, figs. 1, 2; XIII, figs. 5, 6).
? *Cirroteuthis meangensis*, Lo Bianco (1903, pp. 141, 173).
*Cirroteuthis meangensis*, Robson (1926*a*, *passim*).

*Holotype.*—In Brit. Mus.
*Specimen seen.*—The type.
*Distribution.*—Off the Meanjis Islands, 4° 33′ N., 127° 6′ E., in 500 fms. (blue mud) and North of the Kermadec Island (28° 33′ S., 177° 50′ W., in 600 fms. hard ground) (Hoyle); ? off Positano, S. Italy, in 601 fms. (2300 m., wire) (Lo Bianco).

*Description.*—It is very unfortunate that Hoyle did not figure the larger of his two specimens in its entirety. The only complete figure we have seems to be that of the small Kermadec specimen. I have been unable to check or amplify the original in any important respect as the type is very much mangled and the other specimen is missing. The body seems to have been subglobular, at least in the young. The interocular width exceeds the apex-eye length. The eyes are prominent, the head little differentiated from the body. The interocular width exceeds that across the body. In the young the apex of the body seems to have been drawn to a blunt point. The arms in the type are in the order R 1.2.4.3, L 1 = 2, 3 = 4, though there is little difference between them except in 3 R. There are 60–70 suckers in all. The largest are 1 mm. across. Though there are no figures from which we could compute the body-length, I assume this to have been about 25 mm. in the type and the diameter of the suckers 4% of that figure. The cirri are short, stout and conical; the largest are twice as long as the diameter of the suckers. On the ventral

arms they commence between the fourth and fifth suckers and extend to the fiftieth; on the dorsal arms they commence between the sixth and seventh suckers and extend to the fifty-fifth. On the ventral arms there are 21, on the dorsal, 9 suckers beyond the cirri. The web attains a maximum depth of 90% in the type (dorsal arm). The fins in the young were oval with a narrow line of insertion. Hoyle says

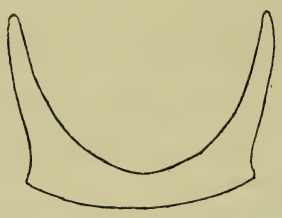


Fig. 22.—*Grimpoteuthis meangensis.* Shell-vestige.

they were about equal in length to the breadth of the body. In the young specimen (Pl. IX) they were smaller. Just above the base of each fin Hoyle found a pore of unknown function. The colour of the body was creamy white, of the arms and web deep madder brown. The mantle-aperture is very small and fits closely round the base of the funnel, which is small and bluntly conical. The shape of the shell-vestige (fig. 22), as figured by Hoyle, is not quite accurate. The measurements of the type-specimen are greater than those shown, the dimensions being :—

| | |
|---|---|
| Hoyle (fig.) | 25 × 15·5 |
| Type | 24 × 18·0 |

The general shape is that of a low hoop. Seen in profile the inner edge is rounded and U-like. The outer edge is, however, angular, this appear-

Fig. 23.—*Grimpoteuthis meangensis.* Mandible. × 4.

ance being due to the flanging downwards of the edges at the bottom corners, four small triangular projections being thus formed. The vestige is oval in section in the middle of the limbs, becoming very much flattened distally. I am unable to discuss Hoyle's statement that in the smaller specimen the vestige was "curved in the horizontal plane in which lies the longitudinal axis of the body," whereas in the adult (?) "it lies in a vertical plane." Hoyle did not describe any parts of the pallial or internal anatomy. In the very fragmentary remains of the larger specimen I have found a normal, well-chitinized dorsal mandible

with a very prominent beak, the remnants of the buccal bulb, on which I could find no radula, and a few large elongate eggs measuring 12·2 × 6 mm. Some of these eggs have longitudinal ribbings or flutings on the outside as in *Stauroteuthis syrtensis* (Verrill, 1882, p. 384).

*Remarks.*—It is a pity that there is so much uncertainty about the characters of the adult of this interesting species. The angular form of the cartilage allies it with *G. glacialis* (Robson). The identity of the young specimen recorded by Lo Bianco in the Mediterranean is very doubtful. Lo Bianco only alludes to the long fins, which are obviously an insufficient basis for identification, and admits that the diagnosis is not exact.

### **Grimpoteuthis caudani** (Joubin).

*Cirroteuthis Caudani*, Joubin (1896, p. 247, text-fig. 7).
? „ *grimaldii*, *id.* (1912*a*, p. 1).

*Holotype.*— ? In Zool. Dept. Univ. Lyon.

*Distribution.*—Only known from the type-locality 44° 36′ N., 4° 25′ W. (Bay of Biscay), mud, in 355 fms.

*Description.*—Joubin did not actually describe the young and very badly damaged specimen which is the only representative of the species. His drawing is "forcément schématique," and I am quite uncertain as to how far one can use it as a basis for redescription. The eyes are enormous, the body very short, its greatest length being about $\frac{2}{3}$ of the interocular width. The body is more or less rectangular, the fins (terminal) being at the apical ends. They are small with parallel sides; their length is about $\frac{1}{3}$ of the interocular width. The cirri are very small. The funnel is long and slender. The pallial aperture is narrow, but not closely adherent. These are all the particulars which can safely be given.

*Remarks.*—This might well be a young form of *G. grimaldii* (see p. 148). I do not think it is very happily compared with *Cirroteuthopsis massyae* by Grimpe (1920, p. 233).

### **Grimpoteuthis plena** (Verrill).

*Cirrhoteuthis plena*, Verrill (1885, pp. 404, 446, Pl. XLII, fig. 3).
*Cirroteuthis plena*, Robson (1926, *passim*).

*Holotype.*— ? Mus. Comp. Zool. Cambridge, Mass.

*Distribution.*—Only known from the type locality 37° 35′ N., 71° 18′ W., in 1073 fms. (grey ooze, bottom temp. 38° F.).

*Description.*—The body is broad, the interocular width being 100% of the length. It is broadly rounded posteriorly and is distinctly long (about 35% of the total length). The head is very short and not delimited from the body. The eyes are relatively small. The arms are in the order 1.2.3.4 and are 67% of the total length. There are about 55 suckers on the dorsal arm, of which about 30 are intravelar. The suckers "sometimes show a slight tendency to become alternate," an observation which has never since been made of any Cirromorph. The suckers attain a maximum diameter of 4·3%. They are usually separated by interspaces "about equal to their own diameter." The cirri are only a little longer than the diameter of the suckers (3–4 mm.), and they

stand " nearly opposite the suckers." The web seems to have the formula ABCDE. At its deepest it is 56% of the arms, E being half the depth of A. The fins are about half the interocular width in length; their edges are more or less parallel until near the end. They are rather anterior in position and lie nearer to the eyes than to the apex. The pallial aperture is small, but it does not closely embrace the base of the siphon. The latter is small but prominent. It projects quite freely from the aperture. The colour (in alcohol) is a " yellowish flesh colour," and the animal is more or less translucent, " the darker internal organs showing through more or less distinctly." The fins are deep brown, darker towards the tips. The oral surface of the web and arms is dark purplish brown, the suckers being dull brownish yellow.

*Remarks.*—Nothing is known of the pallial cavity, the viscera and the shell-vestige. There is more than a passing resemblance to *G. umbellata*, and it may ultimately turn out that these forms are very closely related.

**Grimpoteuthis hippocrepium** (Hoyle).

*Stauroteuthis hippocrepium*, Hoyle (1904, p. 6, Pls. 1, fig. 1; 2, fig. 2; 3, figs. 1–4).

? = *Cirroteuthis umbellata*, Joubin (1920, p. 15).

*Cirroteuthis hippocrepium*, Robson (1926*a*, *passim*).

*Holotype.*—In U.S. Nat. Mus.

*Locality.*—S.W. of Malpelo Island, 2° 35′ N., 83° 53′ W., in 1823 fms., green ooze.

*Description.*—The body is long for a Cirromorph, being 23 mm. from the apex to the mantle-margin and perhaps 30 mm. to the centre of the eye, which would give a body-index of $\frac{30}{80}$ or about 37% of the total length, the arms being thus 63%. The body is said to be " ovoid " (Hoyle, *l.c.*, p. 6). In the figure (Pl. 1, fig. 1) it is curiously rectangular. Its width is 66% of the length. The head ( ? and eyes) was " so macerated that no description of it is possible." These figures are given only very tentatively, especially as Hoyle (obviously in error) gave the total length as about 80 mm. and on p. 7 the length of the first left arm as 90+ ! The arms are " subequal " in length ( ? R 1 = 80+ ; R 4 = 65+). The suckers number about 50 (on each arm ?) and are " of the usual form." They are just over 1 mm. in diameter, *i.e.* about 3% of the mantle. The cirri are very small. The dimensions are not given, but to judge from Hoyle's fig. 4, Pl. 3 they must be very small, as at the level of the web they are shorter than the diameter of the suckers. Their exact distribution is uncertain. The web was not found, but it seems to have been about 50% of the arms. A was much deeper than E. Hoyle says that at the point of the attachment of the web to the arm was a " horny induration " (" cartilaginous nodule " ! explanation of Pl. 3, fig. 4), which he compares with that of *G. meangensis*. The fins are rather small, measuring 18 × 10·5 in the (" about natural size ") figure, (" length of fin . . . 28 mm." (p. 6 !)). They are oblong and rounded ( ?) at the extremity and seem to be wider halfway along than at the base (Pl. 3, fig. 2). The mantle-aperture is very narrow and closely surrounds the base of the siphon. Beyond this narrowness there is no very profound modifica-

tion of the pallio-siphonal mechanism. The funnel is small and subulate, but it projects freely. The dorsal cartilage is said to be horseshoe-shaped. The exact shape is uncertain, as Hoyle's chief figure is seen in side view and his figure 2 (Pl. 3) looks a little sketchy. It was probably of a true horseshoe shape. The colour seems to have been a bright reddish brown on the web and arms, but to have been more or less absent or much lighter on the head, body and fins.

*Remarks.*—Joubin (*l.c.*) thinks that this species may be synonymous with *G. umbellata*. But I do not think there is any basis of comparison available at present.

**Grimpoteuthis mawsoni** (Berry).

*Stauroteuthis* (?) *mawsoni*, Berry (1917, p. 8, Pl. X, fig. 1, text-figs. 1–4).

*Cirroctopus mawsoni*, Naef (1923, p. 675).

*Cirroteuthis mawsoni*, Robson (1926*a*, *passim*).

*Holotype.*—In Australian Museum.

*Distribution.*—Off Mertz Glacier Tongue, Adelie Land, Antarctica, in 288–300 fms.

*Description.*—The body is described as firm, round and almost sepioliform. Its length is a little uncertain; it may be about 37% of the total length (text, calculating apex-eye length as 12 mm.). The width across the eyes is 71% of the body-length, the head being imperfectly delimited from the latter, moderately prominent eyes. The arms are about 60% (less according to text) and are in the order 1.2.3.4. They are equipped with a single series of small close suckers, with minute apertures and a complete series of papilliform intercotyledonary cirri which are only slightly longer than the diameter of the suckers. The web is nearly as long as the arms. It seems to have the formula ABCDE. Between the ventral arms it is very low. There is no intermediate web. The fins are almost as wide as the body. They are squarely truncate at the extremities, the anterior border is straight and at right angles to the main body-axis, the posterior borders being directed obliquely backwards and are continuous with each other as a broad flat fold round the apex of the body. Traces of a similar but narrower tegumentary fold are found in front of the fins. The colour (in alcohol) is a pale brownish cream, the eyes and inner surface of the web slate-coloured. The original integument seems to have been dark red. The pallial aperture is narrow (" very narrow " (Berry), but cf. his Fig. 1) and nearly circular. The funnel is short but tolerably free. No traces of the radula could be found. Berry did not dissect out the shell-vestige.

*Remarks.*—The single specimen known is doubtless very young. Berry elected to treat it as a distinct species on the strength of the presence of a peripheral keel. Though doubtful as to the value of this character, I think the species is otherwise quite distinct. I hardly think we know enough about it to follow Naef in placing it in a distinct genus.

**Grimpoteuthis grimaldii** (Joubin) (? = **G. caudani,** Joubin).

(Text-fig. 24.)

? *Cirroteuthis Caudani*, Joubin (1896, p. 247, text-fig. 7).
*Cirroteuthis Grimaldii*, Joubin (1903, p. 100).
,, ,, *id.* (1912*a*, p. 1, figs. 1–7).
? *Cirroteuthis grimaldii*, Massy (1916*a*, p. 186).
*Cirroteuthis Grimaldii*, Joubin (1920, p. 16, Pls. II, III, IV, XV, fig. 1).

*Type.*—M.O., Monaco. (Holotype.)
*Specimen seen.*—The type.
*Distribution.*—N.N.W. Fayal, Azores, in 1039 fms., and Gulf of Gascony (45° 09′ N., 30° 18′ W., in 986 fms.) (Joubin); ? Andaman Sea, S.W. of Ceylon, Arabian Sea, and off Akyab, Burmah, in 185–540 fms. ("Investigator," five stations) (Massy).
*Description.*—I give Joubin's type-description and Massy's account of her Oriental examples separately, as I regard her identification with a great deal of doubt.
(a) *The type.* I have referred what measurements I could standardize satisfactorily to the length from the dorsal edge of the web to the apex (191 mm.). The general shape is that of "a large egg" (Joubin). The

Fig. 24.—*Grimpoteuthis* (?) *grimaldii*. Shell-vestige. (Mus. Océanogr., Monaco.) Stn. 1450 (1903).

comparison is a little misleading, as the arms are contracted inwards, continuing the convex curvature of the body-profile. The length of the body (Joubin (*l.c.*, Plate IV)) is about 15%–18% of the total length. Its breadth is about 50% of the length from the apex to the edge of the web, the interocular width being rather more. The arms are in the order 1.2.3.4 (or 2.1.3.4). The maximum number of suckers observed was 86. Starting from the mouth there are 3 small suckers very deeply sunk in the skin. They then become rapidly larger (? 6–7 mm. in diameter) up to the 7th. From the 8th to the 36th they are almost the same size (about 3·5 mm.). From the 37th they diminish in size as far as the 45th and finally become microscopic. The cirri are very small. They are minute to start with and become progressively larger, eventually becoming 3 mm. long at the level of the 20th sucker. After that they diminish in size. Joubin (*l.c.*, p. 19) says they are "très ecartés des ventouses, ce qui les différencie de ce que l'on trouve dans les autres espèces du même genre." Joubin says specifically that they are absent at the extremity of the arm. The web has the formula A = D.C.B.E, A and D being 61% of the longest arms and E 46%. The fins are short (Joubin states that it is difficult to take exact measurements) and oval, the line of insertion being obliquely disposed to the long axis of the fin and some-

what shorter than the maximum width of the latter. From Joubin's Plate XV, fig. 1, the anterior border would seem to be markedly rounded, the posterior being almost straight. If we take 37 mm. as the length from the tip to the middle of the line of insertion (Pl. XV, fig. 1, " légèrement grossi "), then the fins are 19% of the apex-edge of web measurement. In length they are probably about a quarter of the interocular width. The mantle-aperture is very small and is just large enough to permit the funnel to emerge. The funnel is stout and conical. The shape of the shell-vestige was ascertained by palpation and seems to have been semi-circular. (See " Remarks " below.) The free extremities narrow down to sharp points. I think the cartilage was oval in section (" ses bords sont à arêtes nettes . . ."). The tissues are very soft and gelatinous. The general coloration is difficult to define owing to changes during preservation. When it was fresh it seems to have been maculated with reddish brown on a pale ground.

(b) *Massy's specimens.* As far as I am able to obtain a satisfactory basis for calculation and comparison I am very doubtful as to whether one can form an opinion on Massy's identification. To begin with, it is not easy to use her figures as a means of comparing her specimens with Joubin's or to find out with certainty how large the animals were. She gives (*e.g.*) for M $\frac{3\,2\,7\,4}{1}$ the body-breadth as 21, the interocular width as 22 and the end of body to dorsal edge of umbrella as 61; the first arms (*ead.*, p. 187) are 140 mm. (!) The result is that in this specimen the length from the apex to the edge of the web is $\frac{61}{140} = 43$, and in the type it is $\frac{192}{217} = 88$. Secondly, Massy's specimens were very variable *inter se*, and especially in " breadth of body," " interocular width " and " fins " (second measurement). Lastly it must be noted that there is a marked difference from the type in the length of the fins (as % of total length) and the number of suckers. Massy (p. 186) says the general contour bears a strong resemblance to that of *grimaldii*, and that the " cartilage " resembles that of the latter fairly well. She says also that the shape " is very like that of *C. meangensis*, except that the outer curves of the 'horseshoe' are less angular." Even with this qualification it does not seem to me that it is possible for the " cartilage " to be " very like that of *meangensis* " and " fairly like " that of *grimaldii* !

*Remarks.*—This is a very characteristic form, in which all distinction of head and body is lost and the cephalo-pallial area is remarkably small as compared with the arms. I do not think Massy's Oriental forms are correctly identified.

I have examined, in addition to the type, the second specimen, obtained from Stn. 1450 (1903). This is remarkably like Joubin's figure of *G. caudani* (see p. 145). It has the same very short body and enormous eyes; but the fins are more or less triangular and occupy all the space between the eyes and the apex of the body. I figure the shell-vestige (text-fig. 24). As I have not seen the type of *caudani*, it is very difficult to say whether either of the specimens of *grimaldii* are really conspecific with the earlier-described form.

**Grimpoteuthis albatrossi,** Sasaki.

*Stauroteuthis albatrossi*, Sasaki (1920, p. 169, Pl. 23, figs. 2, 3).
„ „ *id.* (1929, p. 7, Pl. VII, figs. 3–6; text-fig. 3).

*Type.*—In U.S. Nat. Mus. (Syntypes.)

*Distribution.*—Near Aleutian Is. (Behring Sea); S. Okhotsk Sea; off Kinkasan (N.E. Japan) and Totomi Province, in 918–266 fms.

*Description.*—The body is very short, viz. 18% of the total length (taking Sasaki's 36 mm. as " body length "), plump and " campaniform." If Sasaki's figures are correct, the body is twice as wide as it is long (75 : 36). There is no demarcation between head, body or arms. The eyes are prominent and large. The arms are 82% of the total length ( ? less). There are about 80 suckers on each arm. These are minute at the mouth, become very much larger at the 6th or 7th (8·3%) and thence diminish slowly towards the tips. The cirri are intercotyledonary and " slenderly-conical "; the longest are 4 mm. long. They are continued to the tips of the arms. The web has the formula A.B.C.D.E. and seems to be as long as the arms. The fins are roughly " semi-lunar " (orbicular in young), the posterior edge being straight, the anterior rounded. They measure 23 × 20 mm. and are thus less than one-third the width of the head. The animal is very soft and " choroidal " ( ? gelatinous). The inner surface of the web and arms is a deep purple (sometimes quite black). Externally it is light reddish brown. In the young specimen there is a row of white spots up each arm. The pallial aperture is very narrow and closely embraces the funnel, of which a small terminal portion projects. The funnel-organ is in the shape of a thick **V** to judge from the figure. The gill is of the *Opisthoteuthis* type and has four lamellae aside. The shell-vestige is in the form of a wide and very much flattened **U**, its two arms being each bent into a rather wide angle. The extremities are sharply pointed. The section of the cartilage is crescentic. The radula and mandibles are not discussed; so I infer that the former at least was not present. The posterior salivary glands are " not discernible." The anal valves are rudimentary and the ink-sac is also " not discernible."

*Genitalia.—Male*: Sasaki (*l.c.*, p. 8) says that both the dorsal arms are " hectocotylized." Actually on these arms near the edge of the web there are three suckers very much enlarged. I hardly think it is right to call this hectocotylization, though possibly the enlarged suckers of the male may aid in grasping the female. Such enlarged suckers are, of course, known in Octopods with normal hectocotylus (see p. 15). The penis is small and the vas deferens little differentiated. *Female:* The ripe ovarial eggs are large and measure 10 × 7 mm. The oviduct is single (that of the right side being absent). The spermoviducal gland is enormous and clearly differentiated into two parts. The vagina is thick and short, with a long free portion. The oviduct is long and slender and in the specimen figured by Sasaki there is a prominent swelling of unknown nature about halfway along its course.

*Remarks.*—This is a very distinctive form. The small fins and exceedingly broad body are rather like those of *G. grimaldii*, though the latter is much narrower.

### **Grimpoteuthis glacialis** (Robson).

*Cirroteuthis glacialis*, Robson (1930*b*, p. 375, text-figs. 1–5).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—" Discovery " Station 182 (Schollaert Channel, Palmer Archipelago, Antarctica), in 273–152 fms.

*Description.*—The body is rather short (28%) and only slightly longer than wide. The eyes are prominent and large. The arms are relatively short (71%) and very strong. They are in the order 1.2.3.4. The longest bear about 74 suckers. These exhibit a very peculiar arrangement. The adoral ones are very small, and there is a very gradual increase in diameter up to about the 19th, after which the size as slowly diminishes. The proximal 1–15 or 1–18 are very deeply sunk in the tissues of the arm and are scarcely visible. The largest suckers are 8·3% of the mantle-length. They are very muscular, the inferior chamber and suctorial surface being very well developed. The cirri are intercotyledonary and extend to the end of the arms. They are rather small, the longest being about 6 mm. in length. The web is of the pattern ABCDE, E being under half the depth of A. The web extends up the arms for about three-quarters of their length. The fins are very large, long and deep. They measure 75 × 54, and are therefore almost as long as the head is wide. The maximum depth is along the line of insertion and is about $\frac{2}{3}$ of the apex-eye length. The head, arms and dorsal-mantle area are of a deep bluish purple. The fins and under surface of the body are redder. A very peculiar feature is that the oral surface is coloured the same purple hue as the head, etc. In life there was a circumoral ring of round white patches, each of which was placed astride an arm at the level of the 14–20th suckers. Between this ring and the mouth the web was bright reddish purple, beyond the ring it was a vivid bluish purple. The shell-vestige is very peculiar. It is in general angular and ⋃ shaped. Its base is not unlike that of *G. meangensis ;* but the arms are longer. The vestige is oval in section. The mantle-aperture is very narrow. It embraces the base of the funnel, but is not in contact with it at the sides. The adhesive apparatus is very well developed. The ventral surface of the funnel is excavated to receive the deeply-flanged mantle-edge, and the siphonal locking ridge is likewise deeply flanged and continuous. The funnel is well-developed, prominent and is narrowly conical. It exhibits a thick ∧-shaped funnel-organ. There is no trace of a valve.

*Pallial complex.*—The gills are prominent and globular. They are of the *Opisthoteuthis*-type, and consist of six heavily-folded lamellae. The median pallial adductor is very small and reminds me of that of *G. wülkeri.* Unlike what is found in that form the pallial cavity of *glacialis* has become completely subdivided into two partitions by an excessive increase of the membranous coating of the median adductor.

*Alimentary canal.*—The mandibles are present. They are distinctly delicate and not fully chitinized. They do not differ from those of an Octopodine except in the greater size of the rostrum of the upper mandible and the smaller gular lamella of the lower. The radula is absent. The anterior salivary glands are very small, the posterior absent. The crop is absent. The stomach is equipped with a very well-developed grinding apparatus. The coecum is much larger than the stomach. The ink-sac and anal valves are absent.

*Reproductive organs.*—There is no trace of external secondary sexual characters. The internal organs resemble those of *G. umbellata.* The size

and position of the first accessory gland of the penis relatively to the other two accessory glands is, however, different, and there seems to be an accessory gland of the vas deferens. On the dorsal surface of the penial complex I found a large thin-walled adherent vesicle ( ? Needham's organ). I could find no trace of spermatophores.

*Remarks.*—This species is not unlike *G. megaptera* in external appearance, though the body is longer and the fins of quite different shape, at least from those of the type of *megaptera*.

**Grimpoteuthis wülkeri,** Grimpe.

"*Cirroteuthis umbellata*," Chun (1914, p. 21) (*pars*).
„ „ Ebersbach (1915, text-fig. 1). (See "Remarks.")
*Stauroteuthis wülkeri*, Grimpe (1920*a*, p. 235, figs. 1–3, 5–6).

*Type.*—In the Bergen Museum. (Holotype.)
*Specimen seen.*—The type.
*Distribution.*—35° 46′ N., 8° 16′ W., off N.W. Morocco (Stn. 25, "Michael Sars"), in 1124 fms. Trawl. Only known from the type-locality.
*Description.*—The body is rather widely saccular and is about 23% of the total length (from type-specimen). The maximum width is across the eyes. The apex is bluntly rounded. The head is not demarcated from the body. The eyes are fairly large, but not prominent. They are well under half the length of the body. The arms are in the order 1234 and are about 74% (Grimpe 71%) of the total length. The suckers gradually decrease from the base of the arms (except for the two most proximal suckers) outwards to the extremity. There are about 50–65 on each arm. The cirri alternate with the suckers, and are absent only between the first two suckers and at the extremities. The diameter of the largest suckers is about 2 mm., *i.e.* about 4% of the mantle-length. The cirri do not much exceed this measurement. The web decreases in depth gradually from the dorsal to the ventral arms. Between the dorsal arms it is over 66% of the arms; between the ventral arms it is about 30%. The web has a characteristic shape. It is continued up the dorsal sides of the arms as a very broad membrane, but on the ventral side has scarcely any extension at all, terminating a little above the level of the web in a prominent knob. The web is very like that of *G. umbellata* (Joubin, 1900, p. 23), only differing in the much wider expanse of the dorsal brachial membranes. There is no intermediate web. The fins are remarkably long and measure 54 × 21 (Grimpe) or 56 × 21 mm. (Robson) and easily exceed the interocular width in length. The shape of the fins (Grimpe, *l.c.*, fig. 3) is very characteristic and differentiates the species at once from *umbellata*. The inferior border is more or less straight, whereas the anterior border runs parallel to the body and at right angles to the main axis of the fin for about a quarter of its length, after which it turns sharply and runs at right angles to the body. The outer extremity is, I think, very bluntly rounded and not angular as in Grimpe's figure. The diameter of the fin is well under a half of its length. The mantle-aperture is not tightly appressed to the funnel, but, though narrow, is free of the latter. The funnel is short but prominent and tubular. Grimpe (*l.c.*, p. 237) stresses the fact that its aperture is directed upwards (dorsalwards), *i.e.* in a different direction from that of *umbellata*. The

funnel also does not project as much as in *umbellata*, and as a result the osphradia and inferior edge of the funnel lie within the mantle-border. Grimpe (*l.c.*) states that this species has the remarkable feature of possessing a foveola-like depression under the funnel. I agree with Prof. Grimpe that this area is marked off by its darker colour from the clearer shade of the head, but I must confess that I see in the original little evidence that the depression has anything more than an accidental resemblance to a Decapod foveola. The shell-vestige, as determined by probing it through the skin, is U-shaped. I do not quite agree with Dr. Grimpe (*l.c.*, p. 236) that the arms of the vestige are as much divergent as he indicates. The colour of the dorsal surface of web, head and body is very pale buff (Grimpe, "schmutzig-weiss"). Ventrally it is rather browner. The fins are light brownish purple and the arms dull purple, that colour extending to the periphery of the web. The tissues are very gelatinous.

*Remarks.*—Through the kindness of the Director of the Bergen Museum and Prof. Grimpe I have received on loan the type-specimen which Ebersbach figures in his paper. It is quite clear that this specimen is not referred to in his anatomical description of *G. umbellata*, as it has not been dissected. For an explanation of the identity of Ebersbach's specimens see p. 139.

### (?) **Grimpoteuthis** sp.

(Text-fig. 25.)

*Cirroteuthis* sp., Hoyle (1886, p. 66, Pl. IX, figs. 10, 11).

*Specimen seen.*—Detached suckers in Brit. Mus.

*Distribution.*—Only known from S.E. Pacific Ocean, off N. Patagonia.

*Description.*—All that was left of this interesting fragment for Hoyle to examine was three suckers. The largest of these is 12 mm. in diameter, its orifice being remarkably small (inside diameter about 3 mm.). The sucker seems to have been sunk in the surrounding tissues, as is often the case in *Grimpoteuthis*. Seen in section it is found to have very thin walls and a very weak suctorial chamber. Hoyle's figure does not quite represent the poor development of the latter (see text-fig. 25).

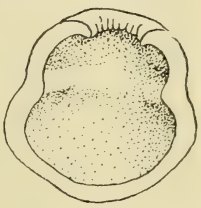


Fig. 25.—*Grimpoteuthis* (?) sp. (Hoyle, 1886). Section of sucker. × *c.* 2·75.

*Remarks.*—There is no clue to the identity of this form. It was found in the form of a large "blubber" floating at the surface, and we owe to the entry in Sir J. Murray's journal the identification as a *Cirroteuthis*. Murray described it as "immense." Hoyle estimated the length as not less than 1·5 m., assuming that the suckers preserved were the largest.

### **Grimpoteuthis** sp.

A very small specimen, 1·5 cm. long, was taken in a tow net 77 miles west of Achill Head, W. Ireland, in 382 fathoms (Hoyle, 1905, p. 98). Hoyle does not describe it. Grimpe (1920*a*, p. 233) thinks it may possibly be a young form of his *Cirroteuthopsis massyae* (cf. p. 160). It was taken in a tow net and may have been captured off the bottom.

(?) **Grimpoteuthis** sp.

*Cirroteuthis* sp. Hoyle (1904, p. 4, ? *C. pacifica*).

A very fragmentary specimen was obtained by the " Albatross " off Tehuantepec (Stn. 3414) in 2232 fms. Hoyle says " so far as can be seen it agrees in many respects with *C. pacifica*," but it differs in the position of the nodule on the arm.

(?) **Grimpoteuthis** sp.

*Cirroteuthis* sp., Hoyle (*l.c.*).

A large piece of web was apparently found on the wire at " Albatross " Stn. 3358 (555 fms.) off Cape Mala, W. Panama. In a note on the drawing of *Froekenia clara*, which was taken by this haul, it is estimated that the specimen must have been at least " × 20 this one " [*F. clara*]. The fragment was not preserved. If the estimate was correct the specimen would have been nearly 5 feet long.

(?) **Grimpoteuthis** sp.

A very large specimen was obtained by the R.R.S. " Discovery " off S. Georgia, and was described (*in lit.*) as " very much larger than " *G. glacialis*. It may have been 3–4 feet long. The specimen was unfortunately lost overboard.

**Grimpoteuthis** sp.

*Stauroteuthis* sp., Hoyle (1912, p. 274).

*Distribution.*—Weddell Sea, Antarctica (66° 40′ S., 40° 35′ W.), in 2425 fms.

*Remarks.*—This form, which is interesting from its locality, was not described by Hoyle. It was in a fragmentary condition and the shell-vestige was not found. From a coloured sketch made (?) on capture the coloration seemed to have been very like that of *G. hippocrepium*, though the colour of the body was more deeply purple. The " gizzard " (? stomach) contained fragments and complete specimens of Crustacea. These have been described by Scott (1910, p. 51), and included the rare abyssal *Pontostratiotes abyssicola*, which had been previously obtained only by the " Challenger " in 2200 fathoms. We are clearly not in a position to discuss the identity of this form, which Hoyle says is " probably either *S. meangensis* or *S. hippocrepium*."

(?) **Grimpoteuthis** sp. (juv.).

? *Stauroteuthis* sp. juv., Berry (1912*a*, p. 274, Pl. XXXIII, fig. 1).

*Distribution.*—Only known from off San Diego, California, in 191–292 fms., a single specimen.

*Description.*—The single specimen available is obviously young, measuring 30 mm. over all. The body is short and plump. From Berry's figure the width of the body (not interocular) is rather greater than its apex-eye length. The eyes are very large. The arms are subequal and rather more than half the total length (figure). The suckers are very minute and are accompanied by paired cirri as usual. Neither the suckers nor the cirri are described in detail. The web is very thick,

and is nearly as deep as the arms are long. The fins are about a third as long as the interocular width, and measure *c.* 8 × 5 mm. (figure). They are slightly constricted at the base, and are " paddle-like " in shape. The mantle-aperture is narrow and closely encircles the base of the funnel. The latter is very small and broadly triangular in shape. The tissues are " subgelatinous." No other descriptive details are given.

*Remarks.*—The single juvenile specimen was not dissected by Berry, so that we know nothing about the shell-vestige, etc. According to Berry it has certain resemblances to *G. umbellata* and *G. plena.*

### **Grimpoteuthis** sp.

(Plate I, fig. 4; text-fig. 15.)

*Cirroteuthis* " A," Robson (1924*a*, p. 680, text-figs. 49–50).

*Specimens seen.*—Five in Brit. Mus. from off Cape Town.

*Distribution.*—Only known from the above-named locality, in 1400–1000 fms., taken in a trawl on Globigerina ooze.

*Description.*—The body is short and very squat, the interocular width much exceeding the apex-eye length. The body is about a quarter of the total length. The eyes are very large, and are each about 21% of the mantle area. The arms are subequal and 76–69% of the total length. They bear 50–60 minute uniserial suckers. The cirri extend from the mouth to the tip of the arms and are small, the longest being about half as long again as the diameter of the suckers. Both the suckers and cirri are deeply sunk in the tissues of the arms, and the cirri seem to be retractile. The web is equally developed all round and is about 50% of the arms, except possibly in E, which may be shallower. The fins are large relatively to the very small visceral sac, but small when compared with the interocular length. Actually they are under a half the interocular width and about half as wide as long (9 × 4·5 mm.). My statement (*l.c.*, p. 681) that they are " narrow at the base and somewhat expanded distally " is true of one specimen but not of all. The colour is of a uniform light brownish purple. The mantle-aperture is remarkably wide and free for a Cirromorph, and the base of the funnel is easily seen through it. The funnel itself is long, tubular and largely protuberant. On opening the funnel a curious arrangement of the inner parts is found. The inner lining of the funnel is found to be detached from the outer and lies as a narrow tube running from the anus to the siphonal aperture. At first sight this condition appeared to be accidental, possibly the result of contraction on being exposed to preservatives. It is, however, present in all five examples, and on close examination the inner surface of the outer cavity is found to be thickened and does not present the condition we would expect if the original wall had contracted away from it accidentally. This modification is very peculiar and has never before been observed, and I am quite unable to say if it is a definite specialization or due to accident. On the dorsal wall of this inner tube is found a ⊂⊃-shaped funnel-organ. The gills are of the *Opisthoteuthis* type and consist of 8 lamellae. The pallial adductor is very small. The dorsal cartilage is slender and has the shape of a widely flattened ⊂⊃ (rather as in *C. ebersbachii*). The mandibles are normal. The rostrum of the upper is not quite half as deep as the palatine lamella. There is no trace of a radula.

*Genitalia.* All the three males examined had the reproductive organs imperfectly developed, but the three sections of the vesicula were indicated and what may be the accessory penial gland.

*Remarks.*—This characteristic form is represented by what I take to be young specimens. The extremely squat and broad body, subterminal and rather large fins, prominent funnel and tolerably wide pallial aperture are an assemblage of characters perhaps most nearly realized in *G. grimaldii*, though in that form the mantle-aperture is narrow.

### **Grimpoteuthis** sp.

*Cirroteuthis* " B," Robson (1924*a*, p. 682, text-fig. 51).

*Specimen seen.*—One (? sex) from off Cape Town.

*Distribution.*—Only known from the above-mentioned locality, found in 790 fms., on Globigerina ooze.

*Description.*—This is a very small and probably immature form measuring only 14 mm. over all. It has a rounded globular body about as wide as long. The head is very short and the eyes rather prominent. The arms are subequal and exceptionally short, measuring (as nearly as I can say) 6–7 mm., *i.e.* 50% or less of the total length. There seem to be about 28 or 30 suckers on each arm. The cirri are represented by low rounded papillae, perhaps one-third as long as the diameter of the suckers. This condition may be one of immaturity, as Berry's very small example of *mawsoni* had small cirri. The web is continued nearly to the arm-tips on all the arms, which may be a sign of immaturity (cf. Robson, *l.c.*, p. 683). The fins are relatively enormous, their length exceeding that of the body. They are long and paddle-like with more or less parallel sides, the width being rather less than half the length. The mantle-aperture is narrow, but it does not embrace the funnel very closely. The base of the funnel (whether as the result of accident or naturally I do not know) is quite free and visible from the exterior. My statement (*l.c.*) that the orifice is directed " posteriorly " was accurate if we use the correct morphological orientation. In the current usage it was directed " ventrally." Owing to some contraction the orifice is now directed anteriorly. The cartilage was originally described as horseshoe-like. Actually it is more like a wide U, and is not unlike that of *G. umbellata* (Grimpe, 1920*a*, fig. 4). The original has been very much discoloured.

*Remarks.*—The affinities of this juvenile form have been fully discussed (Robson, *l.c.*). I maintain my original opinion that it is a young individual of a (distinct) species allied to, but probably not identical with, *G. megaptera*. The size and shape of the fins are very like those of a specimen in the Monaco collection (Stn. 1150) attributable to that species.

## Genus 3. **Chunioteuthis,** Grimpe, 1916.

*Description.*—The body is broad and short. The cirri are two or more times as long as the suckers are wide. The arms are attached to the main web by an intermediate web. The length of the fins is about half the interocular width. The mantle-aperture and funnel are confluent and have a common orifice. The gills are of the *Opisthoteuthis* type.

*Type of the genus.*—*Chunioteuthis ebersbachii*, Grimpe.

**Chunioteuthis ebersbachii** (Grimpe).

? *Stauroteuthis syrtensis*, Verrill (1885, p. 409) (Grimpe).
*Cirroteuthis umbellata*, Chun (1914, p. 21, *pars*).
*Stauroteuthis* sp., Ebersbach (1915, p. 365 and foll.).
*Chunioteuthis ebersbachii*, Grimpe (1916, p. 357, text-figs. 1–3).
,, ,, Robson (1926, *passim*).

*Type.*—In the Bergen Museum. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Only known from Stn. 70, "Michael Sars," 42° 59′ N., 51° 51′ W. (S. of Newfoundland), in 601 fms. Trawl.

*Description.*—The body is rather short (21%) and broad (index 94%). It is bluntly rounded at the apex. The head is not distinct from the body and the eyes are scarcely prominent. The arms are in the order 1234 and attain a maximum length of 76%. According to Ebersbach (*l.c.*, p. 365) there are 55–45 suckers on each arm, a remarkably low number. The first two are pointed-conical, the next 14–16 broadly conical. The diameter of the largest (7, 8–14) is 12 mm. at the base and about four times larger than at the apex. The suckers gradually decrease in size towards the extremities of the arms, become "pot-like" ("topfförmig") and finally cylindrical. At the extremities the suckers seem to be represented by light-coloured flecks. The first four or five suckers are closely placed. From the fifth outwards the suckers are more widely apart, being separated by half the diameter of the base of the adjacent suckers. From the fifteenth the intervals increase abruptly in size. Distally the intervals are wider (see Grimpe, *l.c.*, p. 358). Cirri are wanting between the first four suckers. In the middle part of the arm they are up to 25 mm. long. Microscopic examination failed to reveal the presence of cirri at the ends of the arms (Grimpe does not say how large this cirri-free area is). The web attains a depth of 66% (Grimpe) or 73% (Ebersbach).* Ebersbach states that there is no "Zwischenseptum"; but Grimpe found a short proximal one reaching up to the 9–11th sucker. Grimpe could not find the tubercle-like swelling on the ventral edge of the arm at the point of insertion of the web. A very remarkable and unusual feature is the occurrence of a small, pointed knob in the middle of each sector of the web on the outside about 55 mm. from the arm base. This is not an artefact (Grimpe). The sectors of the web (Grimpe, *l.c.*, fig. 2) seem to be subequal. The fins measure 25 × 50 mm. Their broadest point is along the line of insertion, the edges converging somewhat to a point (more marked in Grimpe's drawing than in Ebersbach's photograph). Their length is about half the interocular width. The mantle-aperture is reduced to a small circular pore. The funnel is small and does not project through the pallial orifice. This, of course, represents the highest degree of reduction in this group. The funnel-organ is unknown. The *shell-vestige* is relatively broad and broadly V-like. Grimpe (*l.c.*, p. 355) rightly compares the shape with that of *Stauroteuthis syrtensis*. The apical portion is, however, thicker, broader and more rounded. The gills are of the *Opisthoteuthis* type, there being no branchial canal. There are four lamellae on each side. The gills as a whole are rather large, and the filaments are very much

* Ebersbach (*l.c.*, p. 365) says that the apical 5–8 cm. of the arm is free from the web.

folded and interlaced one with another. The median pallial adductor seems to be present, but Ebersbach (*l.c.*, p. 377) is not very clear on this point.

*The digestive system.*—The mandibles appear to be normal, but Ebersbach did not describe them. The radula is completely absent. The anterior salivary glands are present and apparently normal. The posterior glands are absent. There is no trace of a crop. The stomach seems to be well developed and to have a strong cuticle and musculature. There is a " third stomach " and no ink-sac. The liver seems to be bifid at one extremity.

*Genitalia.*—Those of the male alone are known. The first section of the seminal vesicle and the proximal vas deferens are (externally at least) more or less indistinguishable. Unlike *G. umbellata* the second and third sections of the seminal vesicle are long. The accessory spermatophore gland found in *umbellata* (Ebersbach, *l.c.*, text-fig. 17, " gl. acc.") and *G. glacialis*, is absent. The accessory gland of the penis is present in three fairly well-defined sections, and Needham's organ is ( ? ) adherent to the penial complex. There is a moderately prominent penis.

*Remarks.*—This very interesting form has plainly some affinities with *Ch. gilchristi*, Robson. Both show the same extreme reduction of the mantle-aperture through which the funnel does not project, and the same very short vas deferens. They are specifically differentiated by the form of the cartilage, suckers, general build and the presence of an accessory spermatophore gland. The small specimen described by Verrill (1885, p. 409) as *S. syrtensis* may be referable to this genus. Beyond the fact that it has the mantle-aperture reduced to a pore from which the funnel was not projecting there does not seem very much in common.

### Chunioteuthis gilchristi (Robson).

*Cirroteuthis gilchristi*, Robson (1924, p. 204).
„ „ *id.* (1924*a*, p. 677, text-figs. 46–48).
„ „ *id.* (1926*a*, *passim*).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Off Cape Town in 1400 fms. Taken in a reversible trawl. Globigerina ooze. Only known from the type-locality.

*Description.*—The body is very short. It is 16% of the total length, the arms being 84%. I am inclined to think that the maximum width is less than I originally stated (34 mm. approx.), viz. 31 mm., so that the width is 119% of the length. The eyes are very prominent and measure 9 × 9 mm. in diameter or about 10% of the area of the visceral mass. The number of suckers on the largest arm is uncertain as they become very crowded and indistinct towards the extremity of the arm. In my first count (1924) I made out 63, but I think they may be a little less (60). They are set rather widely apart, *e.g.* on the first arms at a distance of 45 mm. from the mouth they are 5·5 mm. apart. The profile of the first 20 differs from that in *Ch. ebersbachii* with which this form has been compared. In *ebersbachii* the first two are " spitzkegelig " and the next 14 to 16 are " stumpfkegelig." In *gilchristi* these suckers are flatter and

less conical. On each arm there is a double row of cirri from the first to the twenty-third or twenty-fourth sucker (level of the web), beyond which point they are absent. These attain a maximum length of 18 mm. They are disposed as usual in pairs between the suckers. The adoral suckers are slightly larger than the two which follow them. After the third there is a fairly rapid increase up to about the eighth, which is 2 mm. in diameter. From this point outwards the size gradually diminishes. The largest suckers are about 2 mm. in diameter and rather feeble. The suctorial area is small and the lower chamber thin-walled. The fins measure 18 × 8 mm. Their length is thus a little over half as wide as the body. The pallial aperture, as in *C. ebersbachii*, is reduced to a small pore from which the funnel does not project. This region of the body is not well preserved, and no details can be given as to the funnel.

*The web* (text-fig. 16).—When I measured this in 1924 I obtained a different series of figures from those which I obtained on re-measuring it. Though it is not easy to give the exact measurement owing to the fragmentary state of the web, it is not likely to have been erroneously measured. Probably as a result of transference from formalin to alcohol there has been some contraction. I give both the sets of figures :—

| | 1924. | 1930. |
|---|---|---|
| A . . . . | 115 | 93 |
| B . . . . | 115 | ?97 |
| C . . . . | — | 98 |
| D . . . . | — | — |
| E . . . . | 105 | 80 |

The web was thus bilateral, with B and C a little deeper than A, which in its turn is deeper than E. The tissues generally are delicate and gelatinous. The web is especially thin. The colour was probably a light opalescent purple. The shell-vestige is in the form of a circular rod bent at a very wide angle, its extremities flattened to form insertion surfaces.

*Pallial cavity.*—This is very much reduced in area as compared with that of *G. umbellata*, etc., and occupies only one-half the width of the visceral sac. The funnel " has a considerable free portion and is extended so as to cover the anus, and is secured to the ventral body wall along the median line." There is a paired funnel-organ, the shape of which was not originally described and is now no longer easy to make out. The gill appears to have four very much folded and abbreviated lamellae a side. It is of the type of *G. umbellata* (Joubin) and *Opisthoteuthis*. The branchial gland and heart are present.

*Alimentary canal.*—(Robson, 1926*a*, fig. 4.) The mandibles are normal, but there is no radula. There is no crop. The stomach, coecum and liver are of normal size, and the stomach is thick-walled with a chitinous lining. The proximal part of the intestine is expanded somewhat (? third stomach). There is no ink-sac.

*The genitalia.*—The single specimen available is a male. The vas deferens is short, as in *ebersbachii*. The three sections of the vesicular seminalis are well developed, the first being small as in *ebersbachii*, which this form resembles in the genitalia. There is a small " accessory gland "

as in *G. umbellata*. There is a large complex of penial accessory glands, in the middle of which the short penis opens. It is impossible, without sections, to distinguish the various elements of this with any clearness, but there is adherent to the anterior surface a rather thin-walled sac, which I assume to be Needham's organ. There is no definite trace of the enlargement of suckers. As I have pointed out elsewhere (p. 15), I do not think the enlargement of the suckers, which is called "hectocotylization" by certain authors, should be given that name.

*Remarks.*—I think that in essential features this form shows the greatest amount of resemblance to Grimpe's *Chunioteuthis ebersbachii* (1916, p. 357). It is quite clear that the two are not conspecific, as the shell-vestige, bodily shape, conformation of the pallial cavity, etc., are unlike; but there is a general resemblance, and I am prepared to treat them as congeneric.

The generic position of the following three forms is uncertain (see p. 133).

**Cirroteuthopsis massyae,** Grimpe.

*Cirroteuthis umbellata*, Massy (1909, p. 4).
,, (*Cirroteuthopsis*) *massyae*, Grimpe (1920*a*, p. 233).
,, ,, ,, Massy (1924, p. 127).
? *Cirroteuthis caudani*, Joubin (1896, p. 247) (Grimpe, *l.c.*).
? ,, sp. Hoyle (1905, p. 98) (Grimpe, *l.c.*).

*Type.*—In Nat. Mus. Ireland, Dublin.

*Distribution.*—50° 31′ N., 11° 31′ W., in 670–770 fms. Trawl.

*Description.*—The form of the body was not described by Massy owing to the softness of the tissues. It is rather short (19%), and according to Massy's figures the interocular width is over twice as long as the body-length (index 203). The arms are apparently in the order 2.3.1.4, and are 87% of the total length. The dorsal arms are "enormously developed . . . they are twice the diameter of the others." Massy could find no modification of the suckers on these arms that might support the idea that the size was in some way an expression of hectocotylization [? see p. 15]. There are 3–4 moderately-sized suckers close to the mouth, followed by 5 very large ones (5 mm. or 8·7% of the body-length). These are followed by suckers with an average diameter of 2 mm., which extend slightly beyond the web, from which point they become gradually smaller. They are "very minute" at the tip of the arms. Proximally the suckers are very close together, the largest ones also touching each other. The intervals between them gradually increase, however, and "in the centre of the arm the intervals are twice the diameter of the adjacent suckers." Near the margin of the web they are equal to the diameter of the adjacent suckers, and more distally they are again in contact. There are about 80 suckers on the longest arms, of which about 30 are in the velar area. The suckers have a well-marked elevation above the surface of the arms. The suctorial portion is, as in most Octopods, lined with radiating ridges "which look like shallow pointed teeth." The *cirri* seem to be first discernible without a lens at the level of the largest suckers, and "are

longest throughout the central third of umbrella region." They seem to disappear at the level of the 12th sucker from the tip of the arm. In length they do not seem to exceed the diameter of the largest suckers. Each pair is always placed on a level with the individual suckers, and does not, as usual, alternate with them. The web is of the ABCDE form. It is 75% of the dorsal arms and 66% of the ventral. As in *G. umbellata* (Joubin, 1900, p. 23) there is a hard nodule on the edge of the web close to the ventral side of each arm. The fins, which are terminal in position, are under one-half of the interocular width in length ($\frac{48}{116}$), and the width of the fins is over a half of their length. Their line of insertion is narrower than the maximum width ($\frac{17}{99}$). The anterior edge is curved, the posterior one straight. The pallial aperture is just wide enough to allow the large and prominent funnel to project. The funnel is about 30 mm. in width at its base, and it is 38 mm. long. The shell-vestige is saddle-shaped. Massy also describes the fin-" cartilages " (see p. 129), which seem to be triangular and elongate, with a straight posterior margin. The integument is soft; the colour is a uniform brown madder, the fins being lighter and the oral surface of the free parts of the arms mauve. The suckers are dirty white.

*Remarks.*—The relationship and generic position of this form are somewhat obscure. The original identification (*Cirroteuthis umbellata*), which was made by Hoyle, is clearly erroneous. Grimpe evidently thought that it had something in common with *megaptera*, though it differed in the arrangement of the suckers. I am not sure (p. 142); but I believe that *megaptera* has a differently shaped shell-vestige. Grimpe extends his comparison of *megaptera* and *massyae* to other characters. I am very doubtful as to the significance of the arrangement of the cirrhi. Massy in her later comments (1924, p. 128) on this matter remained quite uncertain whether the latter was due to preservation or natural, and quite rightly remarked that it is a question which can hardly be definitely settled in the case of a single individual. I hold precisely the same view, though I have never seen the condition in question, and, if it were produced as a result of preservation, one would expect it to occur more often. I do not favour Grimpe's suggestion that the Biscayan *caudani* (Joubin, 1896) may be the same as this form, especially as Joubin says that the cirri " paraissent alterner avec des ventouses " . . . ! The only other specimen like it is that of *C. plena* (cf. p. 145). The type of *caudani* was a young specimen in a damaged condition, and it was very imperfectly described. It differs in several important features from *massyae* (cf. p. 145), and looks to me more like a young example of *grimaldii*. The same uncertainty is attached to Hoyle's small specimen from off Achill Head (*id.* 1905, p. 98), which Grimpe thinks may be an early stage of *massyae*. Grimpe (*l.c.*, pp. 232, 233) was of the opinion that this form should be placed in a separate subgenus on account of the cirri (*Cirroteuthopsis*).

### **Cirroteuthis ( ? ) hoylei,** n. sp.

*Cirroteuthis magna*, Hoyle (1886, p. 56 (*pars*), Pl. XI, figs. 3–5; Pl. XIII, figs. 3–4).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—" Challenger," Stn. 298, 34° 7′ S., 73° 56′ W., in 2225 fms., blue mud.

*Description.*—The specimen is very mangled, and I give the various proportions subject to considerable reserve. The total length is about 155 mm., of which the pallio-cephalic area constitutes 24%. The head width is 70% of the body-length. Uncertainty as to whether Hoyle's figure (Pl. XI) is based on a specimen in good condition makes it difficult to speak with certainty as to the relative width of head and body. In its present condition the two are about the same width (unlike *magna*); in Hoyle's figure the head is narrower than the body. The arms are in the order R ?3 = 4, 1 = 2, L 2.1 = 4.3, but the length is uncertain. They are about 79% of the total length. The suckers are very small (2·3%). The cirrhi are longer than in *magna*, viz. 14 times as long as the diameter of the suckers. They commence at about the level of the 3–4 sucker interval and are continued up the arm for about 67% of the length of the latter ($\frac{7\,5}{11\,2}$); (in *magna* they extend for about 60% of the length). The web is thin. It is very mangled and fragmentary. Hoyle rather oddly does not show it as like that of *magna*, *i.e.* as having an " intermediate web " and the asymmetrical development in each sector. I can find nothing on which to base an opinion. Nor can I state the dimensions and form of the web. The fins in Hoyle's figure are large and paddle-like, the length about 1½ times the interocular width, the breadth about half the length. In the specimen as it now is I find the fins are about 42 × 10, *i.e.* more or less as in Hoyle's description of *magna*, but they are of a different shape, having a far wider line of insertion. The shell-vestige was figured by Hoyle (Pl. XIII, figs. 3–4) and is saddle-shaped. It is unfortunately not preserved. From Hoyle's figures it was not so markedly constricted in the middle as that of *magna*, and at the same time it is much deeper.

*Remarks.*—Having in view the defective state of preservation of the only specimen and the somewhat questionable nature of Hoyle's figure, I am naturally a little doubtful as to all the details of this form. I think, however, that (1) the shell-vestige, (2) size and distribution of the cirrhi, (3) size of the suckers and (4) general shape differentiate this clearly from *magna*. After all, the chances against two specimens of an abyssal form, one from near the Crozets, the other from off Valparaiso, being both referable to the same species are fairly considerable.

### **Cirroteuthis ( ? ) magna,** Hoyle.

*Cirroteuthis magna*, Hoyle (1885, p. 233).
,, ,, *id.* (1885*a*, p. 109).
,, ,, *id.* (1886, p. 56 (*pars*), text-fig. 2, Pl. XII; Pl. XIII, figs. 1–2).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—" Challenger," Stn. 146, 46° 46′ S., 45° 31′ E. (between Prince Edward I. and the Crozets), in 1375 fms., Globigerina ooze.

*Description.*—The animal is of a very great size, measuring 1155 mm. over all. The body is relatively small (about 15% of the total length).

Hoyle says that the body is oblong, " about twice as long as broad." He gives, however, the following measurements :—

End of body to eye, 175 mm.
,, ,, mantle-margin, 163 mm.
Breadth of body, 125 mm.

Whichever measurement we take for " length " it does not seem that the body is half as wide as it is long. One might put the width-index at 71%. The interocular width is 57% of the body. The head is not demarcated from the body, and is obviously narrower than the latter. The eyes seem to be of moderate size. The arms are subequal according to Hoyle and in the order R 1 = 2 = 3.4, L 4.3.1 = 2. After making careful measurements I find they are regularly in the order 1234 or 1 = 234, though with little difference. The arms are remarkably slender for a Cirromorph and more like those of an Octopod. The suckers are small (4·5%). They commence about 1 cm. from the mouth. " The first four lie pretty close together within a space of less than 2 cm., after which they gradually become further separated, an interval of 2–3 cm. intervening between each two; about two-thirds along the arm they stand closer together and are very large, but after this they again become smaller and stand in close contiguity with each other." The basal part of the sucker is very thin-walled. The cirri commence at about the 4–5th suckers. They gradually increase in length until halfway along the arm, where they attain a maximum length of 80 mm. or ten times the diameter of the suckers. After this they decrease in length and cease at the level of the edge of the web on the ventral side of the arms. Each arm is independent of the main web, and is connected with it by a vertical membrane or " intermediate web " (Hoyle) that is attached along the dorsum of the arm. This intermediate web has the form of the segment of a very wide circle, the arms held horizontally being the chord, and the line of junction with the main web being the arc. It therefore follows that the web, when the arms are all stretched horizontally, sags downwards in each sector. Each sector of the main web is attached along the whole anterior edge of the arm beyond the point where the intermediate web ends. On the posterior edge of the arm it does not pass that point. The web has the formula A. ?B = C.D.E, and A is 68% of the arms, E being not much more than half the depth of A. I believe the " intermediate web " is produced by the main web between each arm becoming progressively wider and the parts on each side of an arm immediately adjacent to the latter becoming adherent by their dorsal surface. The fins are " obovate " in form, about 200 × 76 mm. in size. They are thus twice as broad as the head and rather less than three times as long as they are broad. The insertion line is shorter than the region of maximum width, and in the figure the fin is shown as increasing abruptly in width. The pallial orifice is but little wider than the base of the funnel. The latter is long, conical and protrudes freely from the mantle-aperture. The colour was originally " rose " (entry in von Willemoes-Suhm's journal). The jaws were evidently thick and strong. The inferior mandible is normal and has a broad descending lamella; the superior has a strong beak, and the rostral lamella is more than half as deep as the palatine.

I could find no trace of a radula in the somewhat mangled buccal bulb. The gills are of the *Opisthoteuthis* type, and have five filaments aside.

*Remarks.*—The affinity of this species to the preceding (*C. hoylei*) is discussed on p. 162. For shell-vestige cf. p. 162.

### Genus 4. (?) **Froekenia,** Hoyle, 1904.

Cirroteuthids with semi-circular shell-vestige and no web between the arms.

*Type of the subgenus.—Froekenia clara,* Hoyle.

*Froekenia* was proposed as a generic name for a small Cirromorph taken in the E. Pacific. There was only one specimen. Though it had all the appearance of a normal member of the group it had " no connecting membrane between the arms." When the specimen came into Hoyle's hands it was in a very decayed condition, and one might well be excused for questioning whether he could have been certain about the web. However, the specimen was accompanied by a coloured sketch made immediately after its capture, in which the web is plainly absent. The sketch bore a note by A. Agassiz—" like a *Cirroteuthis,* but no film " (*i.e.* web). I think with Hoyle that we may infer that the type had no web *when landed.* Whether it was damaged in capture or whether its absence was a normal condition is another matter. There is no other feature that seems at all novel, except perhaps the long and very attenuated arms. The animal has a superficial resemblance to the extinct *Palaeoctopus.*

#### **Froekenia clara,** Hoyle.

*Froekenia clara,* Hoyle (1904 p. 7, Pl. 2, fig. 2; Pl. 3, fig. 5).

*Holotype.*—In U.S. Nat. Mus.

*Distribution.*—Off Cape Mala, Panama (W.) in 555 fms., green sand.

*Description.*—The body is ovoid, the apical extremity being rather pointed. It constitutes rather more than 20% of the total length. The head is short, the eyes rather prominent but not noticeably large. The arms are long and slender, tapering very gradually to the ends. They are subequal, no complete measurements, however, being available. The suckers are very closely set and are " imbedded in much soft connective tissue." The number on the arms is unknown. The cirri are intercotyledonary and a little longer than the diameter of the suckers and " rather stout and blunt." The web is absent between all the arms. The fins are rather longer than the body is wide (figure), and " subelliptical " in shape. The posterior margin is more or less straight, the anterior curved. The shell-vestige is " almost semi-circular," and is pointed at the extremities. No other satisfactory details are known. The ovoid body with a forward prolongation seen within the mantle-cavity in the sketch (Pl. 2, fig. 2) is vaguely suggestive of the ink-sac.

*Remarks.*—The shell-vestige is rather like that of *Ch. gilchristi,* though it is more U-like.

### Genus 5. **Cirrothauma,** Chun (? 1914).

Most of the suckers are modified, probably to carry light-organs. The suctorial chamber is obliterated, and the sucker is borne on a spindle-

shaped stalk containing a light-organ (?). The eyes are degenerate and devoid of a lens, ciliary body and optic ganglion. The animal is completely gelatinous and semi-transparent.

*Type of the genus.—Cirrothauma murrayi*, Chun.

The name of this genus and a description first appeared in Chun's "Promotions-Renuntiations" thesis, "*Cirrothauma*, ein blinder Cephalopod." This work bears no date of publication, though it bears the name of the printer. It is doubtful whether it is a "publication" within the meaning of the International Rules. It is dated by Thiele (1915, p. 490) as 1911. The later date (1914) must be given as that of publication.

**Cirrothauma murrayi,** Chun.

*Cirrothauma Murrayi*, Chun (1911 (?), p. 5).
,, ,, *id.* (1914, p. 22, text-figs. 7–11).
,, ,, *id.* (1915, p. 538, text-figs. 71, Pls. XCII, XCIII).
,, *murrayi*, Robson (1926*a*, *passim*).

*Type.*—? In the Bergen Museum. (Holotype.)

*Distribution.*—Only known from the type-locality, "Michael Sars," Stn. 82, 48° 24′ N., 36° 53′ W., in 1641 fms. (wire).

*Description.*—The body is long and slender, its median width being about 50% of the length and the interocular width about 67%. The body is about $\frac{1}{5}$ of the total length. The arms are in the order 2.4.1.3. They seem to have been thick at the base and gradually tapering to the ends. They are about 75% of the total length. The first six suckers on each arm are small and sessile. They are succeeded by a number of remarkable suckers of a type quite unknown in the Octopoda. The suckers themselves are "flattened and devoid of the sucking-pit" and "evidently out of function." They are borne on long thick spindle-shaped stalks of a gelatinous substance. The gelatinous stalks contain longitudinal and circular muscle-fibres, and in addition a very curious and somewhat enigmatic structure placed in the stalk at the proximal third. Sections of these organs reveal a structure which is compared by Chun (1914, p. 25) to that of a light-organ. In the middle region of the arm the stalks are 4–5 mm. long, but towards the extremity of the arms and towards the mouth they gradually decrease in size. There are 36 suckers on each arm. Slender and transparent cirri alternate with the suckers, the longest of them being 7 mm. The web seems to be equally developed in all the sectors. Chun does not allude to an intermediate web. I do not know if it may not be indicated in his second figure of the web (1915, Pl. XCIII, fig. 1). The web seems to have been about 90% of the arms (fig.). The fins are large and flabellate. Their length is about one and a half times the head-width, and their breadth about half their length. The line of insertion is about half the maximum width. The mantle-aperture is just large enough to allow the funnel to protrude. The funnel itself is long and rather slender. The mandibles seem to be present (Chun, 1915, Pl. XCIII, fig. 1). The eye is very small and is coated over with a thick layer of tissue. It has been very fully described by Chun (*l.c.*), and it is plainly degenerate. There is no lens, the retina is reduced, the optic nerve is very thin, and the optic ganglion is reduced to a faint thickening of the nerve. Behind the eye is developed

a remarkable large pigmented body which is apparently a sinus venosus. The white body persists, but is very thin. The specimen was perfectly gelatinous and semi-transparent. The body was of a faint violet colour, but the parts round the mouth, the oral region of the arms, and the web are " purple chocolate " in colour. There are no chromatophores except a large rhombic one on the ventral side between the fins.

*Remarks.*—This is a very remarkable form. It is the only form of Octopod with degenerate eyes, and the transformation of the suckers into what seem without much question to be light-organs is unique in the Cephalopoda. Finally it seems to represent the most extreme condition of muscular degeneration seen in the Cirromorpha. The structure seems otherwise to be normal; but Chun did not open the mantle-cavity nor dissect any of the internal organs.

### Eggs and Embryos of Cirromorpha.

Verrill (1885, p. 410) described a number of eggs some of which contained embryos. They were obtained from depths of 428–1106 fathoms at " Albatross " Stations 2051, 2072, 2205, 2209, 2210, 2212, etc., and were attached (? singly) to Gorgonians. The embryos have " a well-developed body rounded behind with relatively large, rather broad lateral fins . . . as long as the breadth of the body . . . the eyes are relatively large and prominent, or somewhat stalked." The suckers are uniserial and the web is very poorly developed, " the arms being free nearly to the base." The funnel is prominent and the pallial aperture simple and small, but larger than in *Stauroteuthis syrtensis*. The eggs are contained in an elliptical case about 25 mm. long. The case is strong but flexible. It is often somewhat irregular " on the sides that are attached to the coral-branches." The outer surface is rough and uneven. The egg is found to be much smaller than the interior of the case and is covered with a firm, smooth, transparent shell. The colour [? of the egg] is orange or salmon.

There are in the British Museum a number of eggs that are certainly referable to Cephalopods and may very well be either those of Cirromorpha or Bathypolypods. They are as follows :—

Type A (Plate 1, fig. 2).

Four eggs attached separately to a submarine cable; obtained in 10° 45′ S., 121° 8′ E., in 700 fathoms. The cases are smooth, tough and flexible and are almost tubular, measuring 32 × 9 mm. The proximal end is drawn out into a short, fine stalk. They vaguely remind one of those of *Paroctopus digueti*. They were described in MS. notes as " colourless and opaque."

Type B (Plate 1, fig. 3).

2 sets from a submarine cable in 900 fms., 39° 4′ S., 163° 58′ E.
1 set from a submarine cable, depth and locality unknown.
1 set from a submarine cable, 37° 50′ S., 164° 30′ E., in 770 fms.

All these are narrowly elliptical and measure *c.* 25 × 13 mm. They are smooth and the case is tough, horny and of a faded purple colour.

They are attached separately by a short fine stalk. None of the cases which I have opened contain embryos.

### Family 2. Opisthoteuthidae, Verrill.

The morphologically dorso-ventral axis is very much shortened, and the animal is more or less flattened. The arms are almost entirely included in the web. The fins are very much reduced, and the shell-vestige is either a straight or slightly bent rod, or (?) in two parts.

### Genus **Opisthoteuthis,** Verrill (1883).

With the characters of the family.

*Type of the genus.—O. agassizii,* Verrill.

Berry (1918, p. 289) has recognized a distinction between Verrill's *agassizii* and the other known species in the form of the shell-vestige, which he considers to be of subgeneric value. I am rather sceptical as to the value of this distinction (see p. 168).

### Subgenus 1. **Opisthoteuthis,** Verrill.

The shell-vestige is in two parts (?).

#### **Opisthoteuthis (Opisthoteuthis) agassizii,** Verrill.

*Opisthoteuthis Agassizii,* Verrill (1883, p. 113, Pls. 1–11).
„ „ *id.* (1885, pp. 408, 446).
„ „ *id.* (1896, p. 74, figs. 1–5).
„ „ Chun (1914, p. 21).
„ *agassizii,* Robson (1926*a*, *passim*).

*Type.*—(?) Mus. Comp. Zool., Cambridge, Mass. (Holotype.)

*Distribution.*—Off Grenada, W. Indies ("Blake") in 291 fms. (Verrill); "Albatross," Stn. 2196, 39° 35′ N., 70° 03′ W., in 1058 fms. (*id.*); ? Station in 1230 fms. (*id.*); off S.W. Ireland, 49° 38′ N., 11° 35′ W. ("Michael Sars"), in 504 fms. (Trawl on sand and mud) (Chun).

*Description.*—In the type the body is broad, its width being 83% of the length. All Chun's specimens seem to be as broad as they are long. The head is about as wide as the body. The body is rounded posteriorly. The body is attached to the web, except just behind the fins, where it is slightly free and overhanging. The eyes are very large, each being about 25% of the body. The arms are in the order 1 = 4, 2 = 3; they were probably subequal. They carry a single row of small suckers. These are arranged in a very characteristic fashion. The first 5 suckers are very small; the next 5–6 are the largest. They then decrease again and again increase to attain a secondary maximum at the level of the edge of the web. The largest suckers are about 6% of the mantle-length (calculated). None are discontinuously enlarged in the type; but in two of Chun's specimens specially enlarged suckers are found. In one there are 4–5 large ones after the 6th and two suckers at the arm-tip are similarly enlarged. Some of these suckers exhibit what Chun perhaps erroneously calls pathological alterations, being swollen and devoid of an aperture (see "Hectocotylization," pp. 15, 160). The cirri, which alternate with the suckers as usual, are widely separate from the latter along the middle part of the arm. They are small and do not exceed

the diameter of the largest suckers in length. The web is very thick. It attains a maximum depth of 57% of the arms, but it is continued up the arms as a brachial membrane leaving only about one-fifth free. The fins are fairly long, being over half the interocular width in length. Their sides are more or less parallel, though the general form is " oblong ovate." The width is $\frac{1}{3}\frac{7}{0}$ of the length. The funnel projects freely from the mantle-aperture. The mandibles are present in the type, and there is a warty buccal membrane. The colour is chocolate brown above with small scattered roundish spots of yellowish white. The fins are paler brown. The inner surface of the web is dark chocolate brown, the oral surface of the arms being much paler than the web. In his second specimen (1885) Verrill describes " a thickened muscular appendage " on each arm, as in *Grimpoteuthis megaptera* (?).

*Remarks.*—Nothing is known of the internal structures, shell-vestige, etc. Verrill talks of a fin-" cartilage " in each fin and says that these " are not united across the back "; but I think he must either mean the tough core of the fin (p. 16) or the two ends of the (single) median shell-vestige where they come into contact with the fin-musculature. Of course it is possible that the vestige is subdivided in *agassizii*.

### Subgenus 2. **Teuthidiscus,** Berry, 1918.

The shell-vestige is a single rod-like or crescentic structure.

*Type of the subgenus.—T. pluto,* Berry.

#### **Opisthoteuthis (Teuthidiscus) depressa,** Ijima & Ikeda.

*Opisthoteuthis depressa,* Ijima & Ikeda (1895, p. 323, Pl. XXXIII).
„ „ Meyer (1906, p. 183, Pls. XI–XVI, text-figs. I–XVI).
„ „ Meyer (1906*a*, p. 758).
„ „ Doflein (1906, p. 260, fig., *fide* Sasaki (1929)).
„ „ Marchand (1907, p. 381).
„ „ Dollo (1912, p. 131, Pl. III, fig. 5).
„ „ Berry (1918, p. 289).
„ „ Sasaki (1920, p. 170).
„ „ Robson (1926*a*, *passim*).
„ „ Sasaki (1929, p. 10, Pl. VII, figs. 7–9, text-fig. 4).

*Type.*—? In Mus. Coll. Sci., Imp. Univ., Tokyo. (Holotype.)

*Specimens seen.*—Four from Atami, Japan, in Brit. Mus.

*Distribution.*—Okinose (near Misaki) in 250 fms. (long line) (Ijima and Ikeda); Satsuma (391 fms.), Kii Province (587 fms.), Kusakakijima (440 fms.) and Sagami Sea (70 fms.) (Sasaki); Fuku-Ura (82 fms.) (Meyer).

*Description.*—The animal is very much flattened and has the shape of a plano-convex or concavo-convex disc. Sasaki says that rarely it may be " shallowly campaniform." The largest specimen known to Sasaki has a maximum diameter of a little over 200 mm. The body is but faintly indicated on the aboral surface in the specimens I have seen and in the type. In Sasaki's specimens it seems a little better defined. The maximum width (between the eyes) is about equal to the maximum length (eyes to funnel). The eyes are moderate (type) to large (Sasaki).

In the largest specimen I have they are each about 29% of the visceral mass. The arms seem to be in the order 3421 or 3 = 4.21, but they are virtually subequal. They are entirely encased in the thick web and only $\frac{1}{10}$–$\frac{1}{8}$ of the length is free at the tips. The suckers are very small, being about 4% of the distance from the eyes to the pallial aperture in the type. The cirri are $1\frac{1}{4}$–$1\frac{3}{4}$ times as long as the diameter of the suckers; they commence between the first and second suckers and are continued out to the tip of the arms. They seem to be retractile.* The web is extremely thick and fleshy. In the type sector A is $\frac{2}{4}\frac{3}{8}$ of the longest arm, and E is $\frac{2}{4}\frac{7}{8}$, *i.e.* the one is just under 50%, the other just over 50% of the arm length. In one of my specimens this ratio is larger, viz. $\frac{5}{8}\frac{0}{6}$ of the arm. The web and arms show the curious arrangement seen in other forms (p. 131) in which the arms are all turned forwards, making sector A narrow and sector E wide. Sasaki (*l.c.*, p. 10) believes that this is due to the mode of attachment of the web to the arms. On the dorsal side of the arms the web is attached along nearly the whole length, whereas on the ventral side it terminates far more proximally. The fins are very small. In the type they are under one-quarter of the interocular width. From Sasaki's measurement they would be about one-third or more. In my specimen they are one-third to a half. The breadth of the fin is about $\frac{1}{3}$ of its length. The base is usually the widest part, and the borders gradually converge to a fairly marked point. The colour of the aboral surface is light brown (Brit. Mus.) or deep drab (Sasaki). The oral surface is dark reddish violet (Sasaki), dull purple or brown (Brit. Mus.). The type was " predominatingly madder-red." The oral region, cirri and suckers, etc., are lighter. Sasaki says the aboral surface is further decorated with " eight radiate rows of round pink patches running along the arms," and similar patches occur on the upper surface of the funnel and outside the bases of the fins. I have found these in my specimens; but oddly enough Ijima and Ikeda neither mention nor describe them. The shell-vestige has been figured and described by Ijima and Ikeda, Meyer and Sasaki. The first-named gave only a slight account of it. Between the figures of Meyer and Sasaki there is a marked difference. Sasaki figured the vestige of " a type specimen " [sic] (*l.c.*, Pl. VII, fig. 9), which is not unlike that figured by Meyer. That of another specimen, however, shows a definitely angular structure. The vestige is in the form of a very wide ∪ which is made up of six sections each lying at a slightly different angle. That of Meyer is practically a straight rod. Furthermore, Meyer shows an elongate ovoid insertion-area, whereas Sasaki's older specimen has the area shorter and wider. Lastly, the ends are blunter in Meyer's figure. In short, there is a very remarkable divergence in these two accounts which may be due to varietal divergence or to age. The mantle aperture is very small and fits closely round the funnel. The latter projects quite appreciably. The funnel-organ consists of four patches (two large anterior and two smaller posterior ones). The gills have the characteristic structure (p. 124) and are constituted by 8 filaments (4 a side).

*Alimentary canal.*—The mandibles are well developed. The lower has a long gular lamella, the upper a very acute beak and deep rostral lamella (about as deep as the palatine lamella). There is no trace of a

* All the arms bear some enlarged suckers in the male and the cirri on both sides of them are arranged in 3 to 4 irregular rows.

radula. There appears to be a crop-like dilatation of the oesophagus; but I think it must be secondarily acquired, as it is found close to the stomach, not higher up. The coecum is smaller than usual and there is a well-developed third stomach. There is no ink-sac.

*The Genitalia.*—(1) Male organs (Meyer, 1906, Pl. XIV, fig. 17). The vas deferens is short and is followed by three vesiculae seminales, the last of which has a small appendix. The arrangement of these parts is very like that in *Grimpoteuthis umbellata* (Ebersbach, 1915, fig. 17), though the basal accessory penial gland is very small. The glandular mass of the penis is not much differentiated externally. For a full description of these parts see Meyer (*l.c.*, p. 232 and foll.). As Meyer (p. 237) says it is not easy to follow Ijima and Ikeda's account (*l.c.*, p. 334), which is probably erroneous. The spermatozoa seem to be aggregated into short spiral masses 6 mm. long. Meyer (*l.c.*, p. 232) calls these masses "rudimentären Spermatophoren." As they are found in this condition in the "Spermatophore-reservoir" (sc. Needham's Organ), it is likely that fully developed spermatophores are not found. (2) The female organs (Meyer, *l.c.*, Pl. XV, fig. 21). The oviduct is long and fairly narrow. The spermoviducal gland is double. Its fine structure was described by Meyer (*l.c.*, p. 242). The vagina is short and thick. The eggs found in the ovary only measured 3 × 2 mm., but Meyer thought they were not far advanced.

*Remarks.*—Berry (1918, p. 294) suggests that this form is nearly related to his *O. persephone*. The two species differ in (*a*) the funnel-organ, (*b*) the shell-vestige, (*c*) mandibles, (*d*) depth of the web, and (*e*) number of gill-filaments. *Persephone* has, like *depressa*, a radiating system of aboral spots.

### **Opisthoteuthis (Teuthidiscus) pluto,** Berry.

*Opisthoteuthis pluto,* Berry (1918, p. 284, Pls. LXXXI–LXXXV, text-figs. 64–65).

*Type.*—In the Australian Museum, Sydney. (Holotype.)

*Distribution.*—Great Australian Bight (5 stations, F.I.S. "Endeavour"), in 150–450 fms.

*Description.*—The animal attains a large size, the largest of the four specimens measured having a maximum expansion (tip of right dorsal arm to tip of left ventral) of over 1 ft. 9 in. (540 mm.). The body is very much flattened and "so completely confluent with the head, umbrella and arms as to appear externally only as a low, rounded swelling." It is consequently difficult to assess the dimensions of head and body by our ordinary measurements. It seems to be rather longer than wide, the head being rather wider than the body. The arms are subequal in length and scarcely apparent externally. The suckers are uniserial, firm and hard and of moderate size. Numbers 5–7 are usually the largest, the others diminish progressively towards mouth and tip. In a large specimen there are 80–85 suckers on each arm. The cirri are small, as long as or a little longer than the diameter of the suckers. They alternate with the suckers and seem to be "more or less completely retractile" into cutaneous sheaths. The latter extend obliquely inwards almost to the suckers. The web shows a strong bilateral symmetry, owing to the fact that the dorsal arms are so curved that sector A is much

narrower than D. This condition is seen in *O. depressa* (p. 169) and a rather similar bilateral symmetry in *C. mülleri* (p. 131). The web is 66–61% of the arms, and is usually deepest in sector A. The fins are oblong, twice as long as broad and apparently rather more than half the interocular distance in length. The eyes are moderately large. The funnel is long and narrow. It projects very little from the pallial aperture. Its organ consists of two small, narrowly oval pads placed obliquely to each other. The shell-vestige is broadly ◡-shaped. In the area of attachment to the fin-muscle it is first thickened and then tapers rapidly, the outer surface being flattened and slightly excavated. Between the two insertion-areas the vestige is traversed by a rather deep groove. The upper surface is " finely clouded with chocolate and dark slaty gray " with traces of a system of small " oculations." The oral surface is " cloudy chocolate brown " " more or less overshot with dark slaty purple." The suckers and cirrhi are light brownish. The dorsal areolar spots are fully described and figured by Berry. Their fine structure was also investigated (Berry, *l.c.*, p. 289) without any clue to their nature being found except the demonstration that histologically they are not like the rather similar ocelli in various species of *Octopus*. The gills have " eight segments each " (? 4 a side). The lower mandibles are rather curious in the very heavily curved rostral lamella. The palatine and gular lamellae are as usual short. The radula is absent.

*Remarks.*—See p. 173.

**Opisthoteuthis (Teuthidiscus) persephone,** Berry.

*Opisthoteuthis persephone*, Berry (1918, p. 290, Pls. LXXXI–LXXXII, LXXXV–LXXXVIII, figs. 66–67).

*Type.*—In the Australian Museum, Sydney. (Holotype.)

*Distribution.*—Great Australian Bight, S. of Eucla (W. Australia), in 150–300 fms.; 42 miles S. and E. of Genoa Peak, Victoria, in 232–260 fms. (F.I.S. " Endeavour ").

*Description.*—The animal is of moderate size (330 mm. in diameter). The body is " compressed " (? flattened), and, as in *O. pluto*, is so completely fused with the web as to appear merely as a " poorly defined elevation." The form and proportions of the body are not indicated in the figures and measurements. The eyes are rather small. The arms are rather short and subequal. The suckers are very small and practically equal in size over all the arms, only the three adoral and those towards the tip being appreciably smaller than the rest. There are as many as 78 (?) on the first arm. The suckers seem to be more or less retractile. The cirri alternate with the suckers and are very small. The crypts into which they are retractile are very conspicuous, and extend transversely about two-thirds of the way towards the suckers or sometimes obliquely backwards. The size of the cirri is not indicated. The web is bilateral as in *O. pluto*, but the curvature of the arms is not so conspicuous in *persephone*. The web is 67–65% of the arms. Sector A is said to be deepest (" greatest extension usually in front ").

The fins are " minute," their width being about half their length on the average. They are less than one-half of the interocular width. The funnel is very slender. Its organ is similar in shape and position to that

of *O. pluto*, though the components are relatively larger and more slender. The aboral surface of the type and other Victorian specimens is practically colourless or of a dirty grey, except for traces of areolae and light surface streaks of brown. The surface tissues of the oral surface are colourless and transparent. There is a deeper pigmented layer of a dark bluish slate colour. The suckers and cirrhi are light yellowish brown. There is a pale ring-like zone round the mouth. Small specimens from off Eucla have this ring more sharply defined, and there is no evident pigmentation of the aboral surface except for a series of small ocelli running out to the tip of each arm. The shell-vestige is in general like that of *O. pluto*, but relatively shallower, broader and thinner. The fin-attachment is narrower.

*The mandibles.*—The upper one has a distinct ridge along each side of the rostral lamella, and the latter is as deep as or even deeper than the palatine lamella. The radula is not mentioned. There are six filaments in each gill, with an accessory filament on one side.

*Remarks.*—Berry holds that this form is related most nearly to *O. depressa* and *O. medusoides*.

**Opisthoteuthis (Teuthidiscus) medusoides,** Thiele.

*Opisthoteuthis medusoides*, Thiele (1915, p. 538, Pls. XCIV, XCV).

*Type.*—Not traced. (Syntypes.)

*Distribution.*—" Valdivia," Stn. 243 (6° 39′ S., 39° 30′ E., off Dar-es-Salaam), in 218 fms. Trawl.

*Description.*—The original description is very slight, and few measurements are given. There were two specimens obtained. The figures (Pl. XCIV, figs. 1–2) show two specimens in which there seem to be markedly distinct contours. The one is flattened out like an ordinary *Opisthoteuthis ;* the other is contracted. The visceral mass is high and the flattening characteristic of the genus is not apparent. I assume this merely indicates the difference between the " expanded " and " closed " condition referred to by Berry (1918, p. 284). The arms are short and thick, and the web, which is little differentiated in length, is very nearly as deep as they are long. In one specimen the suckers show no appreciable differentiation in size, in the other the 19th and 20th suckers are markedly enlarged. The cirri are somewhat longer than the diameter of the suckers and seem to be retractile. The fins are placed close to the eyes. They are more or less triangular in shape, and their length is just over one quarter of the interocular distance. The funnel is small, and the mantle-aperture fits closely round it. The funnel-organ " scheint von einem mit der Spitze nach hinten gewendeten V-förmigen Wulst dargestellt zu werden," which is quite a different structure from the paired organ in *O. extensa*. The animals are gelatinous and transparent. Externally they are quite colourless; but the oral surface (? Vorderseite) of the web is brown, the arms appearing more or less colourless.

*Remarks.*—This is a very interesting species, and, as Thiele says, does not give the impression of a benthic form. Its medusiform shape and transparent tissues seem to indicate a pelagic mode of life. Thiele compares it with *depressa* and Berry with *persephone*. In *medusoides* the fins and the funnel-organ seem to be of a different shape.

**Opisthoteuthis (Teuthidiscus) extensa,** Thiele.

*Opisthoteuthis* sp., Chun (1903, p. 538, text-fig.).
,, *extensa*, Thiele (1915, p. 537, Pls. XCIV, XCV).

*Type.*—Not traced. (Holotype.)

*Distribution.*—" Valdivia," Stn. 189, 0° 57′ S., 99° 51′ E., (off W. coast of Sumatra), in 420 fms. Trawl.

*Description.*—As far as can be estimated from the figure the body is as long as it is wide. The eyes are small and set widely apart. The arms differ little in length. The dorsal pair are the longest. The arms show the peculiar arrangement noted by Berry in *Teuthidiscus pluto*. The arms are bent dorsalwards so that sector A of the web is narrow and sector E wide. The web thus acquires a bilateral symmetry. The suckers increase in size from the most interior and gradually decrease again towards the extremity. Thiele says (*l.c.*) that Nos. 1–5 " etwas grösser werden." The cirri are small, but are longer than the diameter of the suckers. The web is not fully described and no dimensions are given. It seems to have been about half the length of the longest arms and on the dorsal side of the arms to have been continued up the arms as a distinct membrane. The fins are inserted into the body halfway between the eyes and the funnel. They are very small, being actually under one-third of the interocular width in length. They measure 15 × 10 mm. and are pointed at the extremity. The line of insertion is as wide as the actual fin. The oral surface is dark brown, becoming lighter at the periphery. The dorsal part of arms and web seems to have been much lighter. The funnel projects over 1 cm. from the mantle-aperture. Its organ consists of two closely placed V-formed plates. The gill consists of six filaments. The shell-vestige is present, but is not described.

*Remarks.*—The shape of the body, the size and shape of the fins and the greater degree of flattening differentiate this species from *agassizii*. Berry (1918, p. 289) compares *T. pluto* with it and says the species may be conspecific. The size and proportion of the fins, the form of the funnel-organ, and, I think, the depth of the web seem, however, to distinguish them.

## Suborder IV. INCIRRATA, Grimpe.

(Apteri, *Prosch & Reinhardt ;* Trachyglossa, *Lütken ;* Polypodoidea, *Naef.*)

The body is devoid of fins and the arms of cirri. The shell-vestige is either in the form of paired rods (" lateral stylets ") or absent. There is no funnel-valve. Both oviducts are present and the radula is usually heterodont. A crop is present, except in the Bathypolypodinae. One arm is generally modified in the male as a copulatory organ.

Doubt is expressed elsewhere as to the homogeneity of this group (p. 34). It may ultimately become necessary to remove the Bolitaenidae from their present association with the Argonautida and Heteroglossa. Naef (1921) and Grimpe (1922) adopted a twofold division of the suborder into the Ctenoglossa (Eledonellidae, etc.) and Heteroglossa (Octopods and Argonautids). I have made three divisions by separating

the Octopodidae (Heteroglossa) from the Argonautida, as I believe that the difference between these groups is substantial enough to merit recognition.

(a) *Special Morphology.*

The body is usually saccular, with a well-defined head. Except in the Bolitaenidae it is rather short in relation to the length of the arms. The suspension of the visceral sac, so far as it is known, is always that characteristic of the order (p. 5). The web is nearly always present, though it is sometimes very shallow. It rarely attains a great depth; but is occasionally at least half as long as the arms (*e.g.* in *Bolitaena ijimai* and certain species of *Bathypolypus*. In the Argonautida it displays peculiar modifications. In *Tremoctopus* it is very much developed between the two dorsal pairs and practically absent between the two ventral pairs. The expansion on the dorsal arms principally involves the lateral membranes of the arms. In *Ocythoë* the web, as such, is entirely absent. Dorsal " swimming membranes " are, however, developed on the dorsal and ventral arms. In *Argonauta* this membrane is very much developed on the dorsal arms and is glandular and secretes the " shell." The expanded lateral membranes in *Tremoctopus* are also glandular, and the secretory areas in the two genera are no doubt homologous. In the Argonautid *Alloposus hardyi* and the enigmatic *Heptapus* the oral surface has rotated backwards so that the outer surface of the dorsal part of the web has become largely adherent to the dorsal mantle. The arms bear two rows of suckers in the Argonautida and in most of the Heteroglossa. In the " Eledonid " Heteroglossa and in the Ctenoglossa the suckers are in a single row. There are no cirri. In the Argonautida the suckers on some of the arms are placed on lateral membranes which run down the sides of the arms (see p. 38).

The suckers are always sessile. In certain members of the Argonautidae they are elongate with a stout stem. In the Vitreledonellidae the suckers are unmistakably degenerate and there is no suctorial apparatus, and they are, moreover, borne on and partly imbedded in a prominent gelatinous boss. In many abyssal forms they are small and weak.

There are no fins in the adult. There seem to be definite traces of them in the embryo in more or less the position which they occupy in the Decapoda (Korschelt & Heider, 1900, p. 264), a fact which points very strongly to the derivation of the Octopoda from a finned ancestor, and incidentally suggests that the fins of the Vampyromorpha and Cirromorpha may be true fins and not a secondary development as Dollo and others wish to maintain. The periphery of the body is sometimes found edged with a continuous or discontinuous ridge (see p. 6).

The mantle-aperture is usually wide; but in some of the abyssal Octopodidae it becomes distinctly narrow, and in one or two forms approaches the condition seen in the Cirromorpha (p. 119). In *Amphitretus* the aperture is restricted to two lateral orifices (see p. 57).

The funnel is usually well developed and in the Argonautidae is very large and prominent. There is no record of a valve in any form, except an ambiguous remark of Joubin's in reference to *Vitreledonella alberti* (p. 322).

The funnel-organ is always present and varies very much in shape from an almost rectilinear single transverse band in *Vitreledonella translucida* to a series of longitudinal stripes in *Tremoctopus*.

The adhesive-organ shows a good deal of variation and requires some discussion.

In the Decapoda the organ consists, as we have seen (p. 8) of a " negative " cephalic element and a " positive " pallial element. In certain Egopsida the elements are doubled and there are both vertical and transverse unions. It will be recollected (*l.c.*) that in the Vampyromorpha there is an adhesive-organ of Decapod pattern. In the Incirrata there is a series of modifications leading to a totally different type of organ. This is illustrated in Fig. 2. In *Argonauta* there is a prominent boss on the mantle-edge which fits into a Decapod-like " negative " element on the head. But under the boss is a transverse groove into which the lower lip of the cephalic element fits as a positive element. The same general arrangement is found in *Ocythoë*, but it is specialized by the conversion of the simple boss into a heavily flanged stud. In *Tremoctopus* the positive element on the mantle is lost, and the original lower lip of the cephalic element persists and is elongated as a prominent ridge which fits into a deep negative pallial element. This condition is seen in the Octopodidae, and the cephalic element may become extensive. On the other hand, in some of the Octopodinae it is very weak and seems to afford very little hold. From this account it will be seen that there is a conversion of the Decapod organ (negative cephalic element) into a form with positive cephalic element, and that *Argonauta* in this respect is most primitive in the Octopoda.

*Alimentary Canal.*—There are two simple lips in the Heteroglossa and Ctenoglossa. In *Ocythoë*, among the Argonautida, there seems to be a tuberculate outer lip; but it is not developed to the same extent as the outer lip of some Decapoda.

The *mandibles* do not call for comment. They are nearly always strong and exhibit a well-developed beak, except in *Vitreledonella*, in which they are very weak and somewhat modified.

*The radula.*—I have discussed on p. 9 the occurrence of two distinct types of radula in this group, viz. a more or less simple undifferentiated type and one in which the teeth are markedly heterodont. In *Tremoctopus* all the teeth are differentiated and the process of differentiation is carried still further in the Heteroglossa. In the Ctenoglossa a different form of radula altogether is found. In this all the inner teeth are multicuspidate. In the Heteroglossa we notice in several sub-abyssal forms definite signs of simplification and degeneration, and finally in *Thaumeledone* we find the radula reduced to the rhachidian tooth alone. This matter is discussed on p. 29.

There are usually two pairs of salivary glands, of which the posterior (" poison glands ") is larger than the anterior, except in *Argonauta* and some abyssal Octopodidae. In *Vitreledonella*, in which the alimentary canal is very much modified, the posterior glands alone are found and are fused in the middle line. The Ctenoglossa and Heteroglossa have a well-developed crop which is an abrupt and localized dilatation of the oesophagus. A crop occurs in *Argonauta;* but it is a weak and ill-defined swelling of the oesophagus and far less defined than in *Octopus*.

The stomach has a well-developed grinding apparatus. The coecum, liver (which is composed of a single lobe in all the forms known to me) and intestine do not call for comment. The ink-sac is absent in a good many deep-water Heteroglossa. When present it is embedded in the liver. The peculiar modifications of the alimentary canal in *Vitreledonella* should be noted (p. 321). Anal valves are found; but in some Heteroglossa they are poorly developed.

*Respiratory Organs.*—The group as a whole exhibits the compact type of gill in which the two demibranchs are parallel and enclose the so-called branchial canal. The number of filaments in each demibranch varies from as many as 24 filaments aside (*Ocythoë*) to as few as five (some abyssal Octopodinae). In nearly all there is a tendency for the inner demibranch to be shorter than the outer. This is exaggerated in *Eledonella*, in which the inner demibranch is about half the size of the outer. Finally, in *Vitreledonella* the inner demibranch is entirely aborted.

*Central Nervous System.*—In the Heteroglossa and Argonautida this is very much condensed and all the ganglia are in close and intimate union. A full description of the system is given by Pfefferkorn (1915). In some Ctenoglossa, on the other hand, the system shows a vague resemblance to that of the Vampyromorpha in the distinctness of some of its constituent elements and in particular in the possession of a distinctly indicated brachial ganglion.

*Reproductive System.*—The Argonautida are distinguished from the rest of the group by the occurrence of a striking amount of sexual dimorphism which attains its maximum in *Argonauta*.

1. *Hectocotylization.*—In the Ctenoglossa a certain number of suckers on the third right arm are enlarged in the male. In *Vitreledonella* and *Amphitretus* there are unmistakable signs of the development of an end-organ. In all the Heteroglossa a fully formed end-organ is found consisting of an apical groove usually with thick sides and often spoon-shaped (the ligula). Along the side of the arm the lateral membrane is converted into a half-open gutter (seminal channel) which terminates at the base of the ligula in a pointed tongue (calamus). In *Bathypolypus* the end-organ is enormous. In the Argonautida the third right arm is autotomous and is highly modified. The forms of hectocotylus in that group are described under the various genera. It is enough here to say that the organ is essentially the same in all four genera and consists of a basal length of sucker-bearing arm, of which the suckers are modified and on which lateral filaments may be present and a terminal flagellum or penis.

2. *Internal Organs.*—(a) *Male.* The system consists of (*a*) a main channel which has in all the groups a three-fold division into glandular sections (vesicular seminales) with (*b*) two annexes, the prostate and Needham's organ. In *Argonauta* (Marchand, 1907) the prostate (" accessory gland ") is very small. In *Ocythoë* it is larger, and in all the other forms it is a large club-shaped organ. In the Ctenoglossa Needham's organ is small. I can detect in none of the forms with which I am familiar any resemblances to the Decapoda, unless it be that in *Argonauta* the penis is not nearly so clearly differentiated as in (e.g. *Octopus*).

The structure of the spermatophores, which are usually complicated, has been described for *Eledone* and *Octopus* by Marchand (1913). There

are ordinarily a large number found in Needham's organ, but in certain deep-sea Octopodines they are very large and few in number, and in *Benthoctopus ergasticus* there is only a single enormous spermatophore. (b) *Female.* The female ducts are double and thus retain the primitive condition. The oviducts and vaginae vary very much in size and may be very short and stout, as in *Thaumeledone*, or long and slender, as in some species of *Octopus*. In *Ocythoë* the vaginae are excessively long and tortuous (Sasaki, 1929, p. 27). I believe the size of these organs is correlated with the size of the egg. A spermoviducal gland is always present (see Part I, p. 17, and Sasaki (*l.c.*, p. 31)).

The eggs are very small in the majority of Octopodines and the Argonautida, but in the "Eledonid" Octopodids and Bathypolypodinae they are much larger, and are sometimes as much as 25% of the mantle in length.

In the Argonautida there is evidence of the continued suppression of the vestiges of the coelom (see p. 15). In the female *Argonauta* (Brock, 1882, p. 599) both canals are absent, though Sasaki (*l.c.*, fig. 10) shows vestiges of them in *Tremoctopus*. They may be, and probably are, absent in the Bolitaenidae and Vitreledonellidae. In *Ocythoë*, on the other hand, they are present and function as oviducts (Sasaki, *l.c.*, fig. 8*b*). In this form Sasaki also found egg-clusters fixed to the wall of the renal sacs.

*Shell-vestige.*—I have not succeeded in finding any important deviations from the form of shell-vestige found in the Octopodinae. The vestige occurs in *Tremoctopus* alone of the Argonautida and in none of the Cteno-glossa.

(b) *Systematic.*

Tribe I. Argonautida, trib. nov.

The hectocotylized arm is autotomous, and sexual dimorphism is very marked. The adhesive-organ may be complex and like that of the Decapoda in general plan. The suckers are biserial. The web is highly modified or absent. The radula is homodont or heterodont.

Family I. Argonautidae, Tryon.

The web is only slightly developed. There are no water-pores and no shell-vestige. The radula is "sepioid." The cephalic and pallial elements of the adhesive-organ are paired (see p. 8). The water-vascular canals are absent or rudimentary. The suckers are long and borne on a lateral membrane. A secondary (incubatory) shell is developed on the first arms of the female.

Genus **Argonauta,** Linné.

With the characters of the family.

*Type of the genus.*—*A. argo*, Linné.

A very large number of specific names have been given to forms of *Argonauta*, and there is a very extensive bibliography ranging from the inventories or sale-catalogues of curio-collections to critical zoological descriptions. I am very sceptical as to the value of the bulk of this literature, especially as many of the older figures are very poor.

Since the middle of last century there have been three attempts at an arrangement of the species. (1) Von Martens (1867, p. 103) believed that there are " three constant *types* " (at least in the actual material before him)—*argo*, *tuberculata* and *hians*. Within each " type " there are certain " forms " (forma *mutica*, *obtusangula* and *aurita*) which are discussed below. (2) Tryon (*l.c.*, p. 133) thought that all the species previously described were referable to three " groups " and may not exceed that number of distinct species. His " groups " were *argo*, *hians* and *nodosa*. (3) Dall (1908, p. 225 and foll.) recognized four " groups " (? subgenera), eight species and four species " incertae sedis."

From a careful review of the subject it seems to me that of the described species *argo*, *nodosa* (=*tuberculata* Auctt.) and *hians* are certainly to be maintained, that three others are probably distinct and the rest are indeterminable.

Before proceeding to discuss these various forms it is necessary to say something concerning the variation of the shell and in particular about von Martens' theory that each of his " types " exhibits three main forms which are identical in all three types.

These " forms " are (1) " forma *mutica* " (" lateral edge of the aperture . . . nearly straight, the aperture therefore narrow," (2) " forma *obtusangula* " (" [edge forming] near its inner end an angle which is more or less blunt "), and (3) " forma *aurita* " (" [edge] extends itself into a prolongation called the ear ").

I think it is sufficiently clear that von Martens wishes to distinguish (*a*) a form with edges more or less parallel and straight or lightly sinuous when viewed laterally, (*b*) a form with sides more or less parallel, but having the inner end formed into an angular prominence, and (*c*) a form in which the sides are no longer parallel, but the prominence (ear) seen in (*b*) is strongly developed and curved outwards. Von Martens does not make it clear that the ear may be very strongly developed but not curved outwards. This is a little unfortunate as Martens and Dall both use the term " eared " and " auriculate " without making it plain whether they mean (*b*) or (*c*).

On page 179 are given the measurements, etc., of 18 shells of *A. argo* (six characters). It will be seen that the edge of the shell-lip may be (viewed laterally) in the shape of an obtuse angle, horned (auriculate) or nearly straight, and that viewed *en face* the aperture may be very wide, the width between the " ears " being 61·6% of the length or very narrow (35%). I can find no justification for Dall's statement (*l.c.*, pp. 227–8) that Mediterranean forms show less " auriculation " (width) than others. I have four Mediterranean specimens, of which three are markedly auriculate. Nor can I find that Dall's statement (p. 227) that young specimens of nearly all the larger forms are for a time distinctly auriculate but may become simple in the adult stage, is true of *argo*, in which several of our very large specimens are very wide (auriculate) and some of the small ones are narrow. The mean, maximum and minimum ratio of aperture-width to length of 9 large ones is 38–49%–61 (width expressed as a percentage of the length) and that of 9 small ones is 35–54%–60. Having regard to the small number of specimens and the range in both cases the difference is plainly not significant. There seems to be a marked correlation of size with keel-width, as (p. 179) small

specimens tend to have a relatively wider keel. The sculpture is on the whole pretty constant. Usually the simple ridges (primary and secondary) are distinct and unbranched, but in rather more than half the specimens I have seen there is slight branching, *e.g.* in our series from Cape Agulhas the following are the figures for branched and unbranched ribs :—

| Specimen. | Ribs. | |
|---|---|---|
| | Branched. | Unbranched. |
| 1 | 5 | 59 |
| 2 | 10 | 43 |
| 3 | 4 | 46 |
| 4 | 5 (?) | 44 |
| 5 | 4 | 33 |

There is some variation in the nature of the branching. Usually it is in the form of a simple fork, sometimes, however, it is a double fork or a single fork and two simple rays. On the whole there is not much variation in the carinal knobs or in the colour. I have never seen any truly nodose forms.

| Specimen. | Max. Diam. (mm.) | Aperture, length. (mm.) | Keel-width % aperture. | Between horns (mm.) and % aperture. | Edge of aperture. | Sculpture (S=simple B=double fork). |
|---|---|---|---|---|---|---|
| 1. Simon's Bay 1920.2.20.3 | 280 | 168 | 4·6 | 92(54·7) | Auriculate | S. |
| 2. Philippine Is. (Coll. Broderip) | 260 | 152 | 5·7 | 75(49·2) | Obtusangulate | S.B. |
| 3. do. (Coll. Cuming) | 248 | 146 | 5·4 | 90(61·6) | Auriculate | ,, |
| 4. S. Africa 1907.8.29.27 | 248 | 155 | 4·5 | 74(47·7) | Aur.-obtus. | ,, |
| 5. ? loc. | 238 | 153 | 4·5 | 72(47·0) | Obtusangulate | ,, |
| 6. ? loc. 59.6.21.1 | 236 | 152 | 6·5 | 81(53·2) | Auriculate | ,, |
| 7. Loo Choo 96.1.14.54 | 200 | 152 | 6·5 | 72(47·3) | ,, | ,, |
| 8. ? loc. B. 702 | 163 | 102 | 7·4 | 47(46·0) | ,, | S.B. |
| 9. C. Agulhas | 160 | 118 | 6·2 | ?46(38·9) | Obtusangulate | ,, |
| 10. ? loc. | 153 | 112 | 6·2 | 55(49·1) | ,, | ,, |
| 11. Venezuela M.C. | 148 | 90 | 7·2 | 40(44·4) | ,, | ,, |
| 11*a*. ? loc. | 141 | 98 | 6·1 | 46(46·9) | Nearly straight | S.B. |
| 12. C. Agulhas | 115 | 80 | 7·4 | ?41(35·6) | Auriculate | ,, |
| 13. Malta | 115 | 81 | 8·6 | 36(44·4) | Obtusangulate | ,, |
| 14. Sicily M.C. | 114 | 86 | 9·3 | 41(47·6) | Auriculate | ,, |
| 15. ,, | 112 | 85 | 6·4 | 45(52·9) | ,, | ,, |
| 16. C. Agulhas | 96 | 68 | 9·5 | 38(55·9) | Nearly straight | S. |
| 17. ,, | 84 | 61 | 10·6 | 33(54·0) | Auriculate-obtusangulate | S.B. |
| 18. ,, | 65 | 50 | 12·0 | 30(60·0) | Auriculate | S. |

From the foregoing it will be seen that the degree of auriculation and the extent to which the " ears " are bent outwards is subject to a great

amount of variation which is not correlated with the size of the shell. The contrast between type (*a*) and (*c*) is very marked, and indeed it might be urged that in accepting Martens' view I am neglecting an obvious basis of specific distinction. Nevertheless these shells, whether eared or earless, are homogeneous in size of keel, character of sculpture and size of the carinal knobs, and on that account I think we should base our specific distinctions on those characters rather than on the auriculation.

As Dall's arrangement is the most up-to-date and was based on a critical examination of the older literature and figures, I give below his list with my own comments.

1. *A. grandiformis*, Perry (1811, Pl. 42, fig. 4). This I think is clearly a form of *argo*.
2. *A. argo*, Linn. For the identification of Linné's species see p. 189. Dall recognizes as varieties :—

   *A. argo papyria* (*A. papyria*, Conrad (1854, p. 331, Pl. 34, fig. 1)). As Dall says the lateral sinus is probably obliterated accidentally.

   *A. argo cygnus* (*A. cygnus*, Monterosato (1889, p. 120)). Only very summarily described, but Reeve's fig. 2*c* is cited. Probably = *A. argo*.

   *A. argo* s.s.

   *A. argo var. americana* (*A. americana*, Dall (1889, p. 174, Pls. 43, 64, 67). From the broad keel, few ribs and very prominent carinal knobs, I assume this is a form of *hians*.

   *A. argo pacifica* (*A. pacifica*, Dall, 1869, p. 238; 1871, p. 95). No details of shell are given except that it is "more compressed, and with pronounced auricles." Radula, etc., described. This should be treated as an indeterminable form.
3. *A. bulleri*, Kirk (1886, p. 138, Pl. 4). According to Suter (1912, p. 1066) this is a form of *argo*.
4. *A. nouryi*, Lorois (1852, p. 10, Pl. i). This is probably a distinct species (see p. 198).
5. *A. cornuta*, Conrad (*l.c.*, p. 332, Pl. xxxiv, fig. 2). This differs from *argo* in its wide keel and the ribs; from *nodosa* in the absence of tuberculations; and from *hians* in the possession of narrower ribs. I think this may be a form of *hians*.

   *A. cornuta dispar* (Conrad, *l.c.*, Pl. xxxiv, fig. 3). Status uncertain : ? = *nouryi* or a distinct species (see below, p. 197).

   *A. cornuta* s.s.
6. *A. nodosa*, Solander (1786, p. 96). This is based on a figure of Rumphius' (Pl. xviii, fig. 1), which is rather obscure, but probably = *tuberculata* Auctt. A distinct species.

   *A. nodosa bibula*, Bolten (1798, p. 71). This was based on a figure in Martini (1769, Pl. 18, fig. 160). Its validity is very doubtful and it may be a form of *hians*.

   *A. nodosa* s.s.
7. *A. hians*, Solander (*l.c.*, p. 44) after Rumphius (1705, Pl. 18, fig. B). Clearly a distinct species.

   *A. hians navicula*, Solander (*l.c.*, p. 44) after Rumphius (*l.c.*, Pl. 18, fig. 4). Identity doubtful; it might be *A. argo*, though

the ribs are less numerous and the shell is more oblong. ? A form of *A. nouryi*.

*A. hians* s.s.

8. *A. boettgeri*, Maltzan (1881, p. 163, Pl. 6, fig. 7). I think this is a distinct species.

*Incertae Sedis.*

9. *A. fragilis*, Parkinson (1856, p. 387). Status obscure. "Back narrow" seems to suggest *A. argo*. Dall questions whether it is not an abnormal specimen.
10. *A. geniculata*, Gould (1852, p. 470, Pl. 45). Shell not known.
11. *A. rufa*, Owen (1838, p. 114; Gray, 1849, p. 34). Insufficiently described. (Type not traced.)
12. *A. conradi*, Parkinson (*l.c.*, p. 386). Unfigured and very uncertain. Only $2\frac{3}{8}$" in length. Dall suggests its identity with "*A. dispar*" (? *A. cornuta dispar*).

I have reduced Dall's eight species to six for reasons which are given under the various species. It must be remembered that we know very little about the anatomy of the various species.

### **Argonauta argo,** Linné.

(Text-fig. 26.)

*Nautilus*, Belon (1553, II, p. 378).
„ [*Argonauta argo*] ? Rondelet (1554, XVII, p. 517).
„ Gesner (1558, IV, p. 732).
„ Aldrovandi (1606, III, cap. 3, p. 257).
„ Jonstonus (1650, III, cap. 1, p. 39, tab. x).
„ Bontius (1658, V, cap. XXVII, p. 79).
„ *Nauplius, Pompilos*, Olear (1674, p. 61, Pl. XXXII, fig. 4. An earlier date cited by Naef).
„ Legato (1677, p. 105, *fide* Naef).
"*Nautilio*," Bonanni (1681 (?) p. 142, 3rd plate, fig. 13).
*Nautilus tenuis*, Rumphius (1705 (? earlier ed.), p. 63, Pl. XVIII, fig. A and (?) 4).
„ *maximus* . . . Lister (1688, lib. IV, sec. IV, fig. 556–7).
„ , *Pompilum*, Lochner (1716, p. 70, Pl. 19).
„ *major*, Valentini (1704, II, p. 58, tav. I).
(?) *Nautulus*, Valentijn (1726, p. 581, with Pl. 1, fig. 4 = *Nautilus* sp. cited by Naef with name *N. minor* (where ? )).
*Nautilus*, Kindmann (1726, p. 124), *fide* Naef and Jatta (where ?).
„ *papyraceus* (*?*) d'Argenville (1742, p. 247, etc., t. 8, fig. A.
*Cymbium maximum*, Gualtieri (1742, t. 11).
*Cymbium* ——, Lesser (1748, p. 149, *fide* Naef).
*Nautilus tenuis* . . . non *auritus*, Hill (1752, p. 122 Pl. 7).
*Nautilus Sulcatus* (pars), Klein (1753, p. 3, t. 1, fig. 3).
"*Papier Nautilum*," Knorr (1757, p. 2, t. II, fig. 1. Given as "Ammonia, Knorr 1766" by Naef).
*Nautilus tenuis*, Seba (1758, III, t. LXXXIV, figs. 5–7).
"*Nautilio*," Ginanni (1757, t. II, p. 5, tab. III).
*Argonauta argo*, (?) *cymbium*, Linné (1758, t. 1, p. 708, No. 231).

*Nautilus tenuis*, Petiver (1764 ( ? earlier edn.), p. 2, t. X, f. 1).
„ *papyraceus*, Martini (1769, t. 1, p. 231, Pl. XVII, fig. 157).
" *Nautile papyracée*," Favart d'Herbigny (1775, p. 419).
*Nautilus* ( ?), *Cymbium*, da Costa (1776, pp. 168, 287, t. III, fig. 6).
" le grand Nautile papyracé," etc., Favanne (1780, pp. 707, 709, 710, Pl. VII, fig. A 2, etc.).
*Argonauta argo*, Born (1780, p. 140).
( ?) *Argonauta* ——, Gronovius (1781, p. 281).
*Argonauta argo* Schröter (1783, p. 4, Pl. 1, fig. 1).
„ „ Favanne (1784, p. 57).
*Nautilus*, Schneider (1784, p. 120).
*Argonauta Argo*, Gmelin (1790, p. 3367).
„ „ Shaw and Nodder (1791, t. III, Pl. 101).
„ *argo*, Wolfen (1791, p. 235, *fide* Naef, where ?).
" *Argonaute papyracé*," Bruguière (1792, p. 122. Naef cites 1789 ( ?)).
*Argonauta argo*, Olivi (1792, p. 129).
„ *corrugata*, Humphrey (1797, p. 6).
" *Nautile papyrace*," Cubières (1798, p. 43, Pl. IV, figs. 6–7).
*Argonauta Argo, ? papyracea*, Bolten (1798, p. 70).
" Argonaute papiracé" (sic !), Montfort (1802, t. III, p. 118, Pls. 35, 36).
*Argonauta argo*, Bosc (1802, t. III, Pl. 27, p. 261).
„ —— Montfort (1808, p. 6).
( ?) „ *grandiformis*, Perry (1811, Pl. 42, f. 4).
" *Argonauta argo*," Duvernoy (1816, III, p. 102), *fide* Naef. In the later edition (1849, vol. II, p. 121) there is an article by Orbigny).
*Argonauta Argo*, Schumacher (1817, p. 260).
„ *argo*, Cuvier (1817*a*, II, p. 377, 3rd edn.).
*Ocythoe antiquorum*, Leach (1817*a*, p. 139).
*Argonauta Argo*, Ranzani (1820, Dec. 1, p. 85).
„ *argo*, Lamarck (1822, VII, p. 652), with *nitida* and *tuberculosa*.
„ *Argo*, Burrow (1825, Pl. XII, fig. 1, " 1818," *fide* Naef).
„ „ delle Chiaje (1825, p. 219).
„ „ Ferussac (1825, p. 161, Pl. 14).
*Ocythoë Argonautae*, Blainville (1825, p. 366, Pls. 1–1 *ter*).
*Argonauta Argo*, Payraudeau (1826, p. 172).
„ *argo*, Risso (1826, IV, p. 4).
*Ocythoe antiquorum*, Blainville (1826, p. 192).
*Argonauta argo, compressa*, Blainville (*l.c.*, p. 212).
„ *Argo*, Poli (1826, t. III, pars. 1, p. 4, Pls. XL–XLIII).
„ „ etc., Férussac (1822, I, p. 552).
„ „ Orbigny (1826, p. 137).
*Argonauta* —— Mauriani (1827, p. 390).
*Argonauta Argo*, Broderip (1828, p. 57, Pl. III).
„ „ *uniumbilicatus* ( ?), Costa (1829, p. LXI).
„ *argo*, Sangiovanni (1829, p. 322).
„ „ Deshayes (1830, p. 69 and 1832, III, p. 643).
„ *Argo*, Sowerby (1831, Pl. 277).
„ „ Oken (1835, p. 532).
„ „ Scacchi (1836, p. 18).
„ „ Philippi (1836, p. 240).

*Argonauta Argo*, Rang (1837, Pls. 86–88).
„ *argo*, Potiez and Michaud (1838, p. 2).
„ „ Orbigny (1840, p. 158, Pls. 1–1⁵, 2, 6).
„ „ Cantraine (1841, p. 20).
„ *Argo*, Costa (1841, p. 184, Pl. 13).
„ „ Reeve (1842, p. 309, Pl. CCC).
„ „ Philippi (1844, p. 201).
„ „ Power (1845, p. 369).
„ „ Requien (1848, p. 87).
„ *argo*, Kölliker (1849, p. 67, tab. 1, 2).
„ *Argo*, Gray (1849, p. 31).
„ „ Verany (1851, p. 48, Pls. 17, 18. Hectocotylus figures as *Hectocotylus argonautae*, Pl. 41).
„ „ Müller (1853, p. 1, Pl. 1).
„ „ Adams (1853, p. 25).
„ *argo, minor* (Risso, 1854, pp. 75, 77).
„ *naviformis, papyria* Conrad (1854, pp. 331, 334).
„ *Argo*, Orbigny (1855, pp. 226, 234, Pls. 6 & 7, figs. 1–5).
„ „ Troschel (1857, p. 42).
„ „ Reeve (1861, Pls. II, III, figs. 2*c*, 2*d*).
„ „ Sowerby (1866, p. 263, Pl. 257, figs. 1, 2).
„ „ von Martens (1867, p. 104).
„ —— Garner (1868, p. 97).
„ *argo*, Weinkauff (1868, p. 432).
„ „ Küster (1868, p. 4, Pl. 1, fig. 1), etc.
„ „ Ford (1869, p. 276).
„ „ Targioni Tozzetti (1869, p. 587).
„ „ „ „ (1869*a*, p. 148).
„ „ Lischke (1869, p. 29).
„ *gondola* (?) Lockwood (1877, p. 243).
„ *argo*, Tiberi (1878, p. 160). Hist. notes only.
„ „ Molina (1878, p. 146).
(?) *Argonauta* sp. Anon. (1878, p. 397).
*Argonauta argo*, Tryon (1879, p. 138, Pls. 47–49).
„ *Argo*, Tiberi (1880, p. 5).
„ *argo*, Verrill (1881, p. 113).
„ „ *id.* (1882, p. 364).
„ „ *id.* (1884, p. 247, Pl. XXVIII, fig. 1).
(?) " Paper Nautilus," Lockwood (1881, p. 908).
*Argonauta argo*, Hoyle (1886, p. 69).
(?) „ *bulleri*, Kirk (1886, p. 138, Pl. 4) (*fide* Suter).
„ „ Fischer (1887, p. 335, figs. 117–119).
„ „ Darbishire (1888, p. 371, Pl. III).
„ *cygnus*, Monterosato (1889, p. 120).
„ *argo*, Colombatovič (1890, p. 5, *fide* Naef).
„ „ Carus (1890, p. 457).
„ „ Joubin (1895, p. 9).
? *Tremoctopus hirondellei*, ? Joubin (*l.c.*, p. 10, *fide* Naef 1912*a*, p. 198).
*Argonauta argo*, Jatta (1896, p. 191, Pls. 8, 18).
„ „ Smith (1903, p. 310, fig.).
„ „ Heinrich (1904, p. 14).
(?) „ „ [var]. *pacifica*, Dall (1904, p. 225).

*Argonauta argo*, Marchand (1907, p. 377, figs. 54–56).
„ „ and *pacifica*, Dall (1908, pp. 225 and foll.).
„ *Argo*, Suter (1913, p. 1066).
„ *argo*, Naef (1912*a*, p. 198).
„ „ *Sebae &c.*, Monterosato (1913, p. 387, Pl. XI. Valenciennes MS.).
„ *cygnus, Monterosatoi, id.* (*l.c.*, p. 388, Pls.).
„ *ferussaci, id.* (*l.c.*, p. 389. Valenciennes MS.).
„ *cygnus*, Coen (1914, Pl. 1, fig. 3).
„ *Sebae, id.* (*l.c.*, Pl. 1, fig. 1).
? *Argonauta Monterosatoi, id.* (*l.c.*, p. 23, Pl. 1, fig. 2).
*Argonauta argo*, Pfefferkorn (1915 *passim* and Pl. XIV).
„ *Argo*, forma *mediterranea, Ferussaci*, Gregorio (1915, p. 193).
„ *argo*, Naef (1916, p. 17).
„ „ Wülker (1920, p. 56).
„ „ Naef (1921*a*, Pls. *passim*).
„ „ „ (1921*b* p. 538).
„ „ „ (1923, p. 763).
„ *Argo*, Degner (1925, p. 81).
„ *argo*, Naef (1928, p. 281, Pls. 32–37).
„ „ Grimpe (1928, p. 77, Pls. 3–5).
„ „ Sasaki (1929, p. 23, Pl. III, figs. 8–12, text-fig. 7).

*Type.*—Not traced.
*Specimens seen.*—(*a*) In British Museum.

i. *Complete specimens or specimens without shell.* Three from the Mediterranean; one from N. Africa; one from the Atlantic (?); five from unknown localities.

ii. *Shells only.* Four from Sicily; one from N.W. Italian Coast; one from Simon's Bay, S. Africa, 1920.2.20.3; one from Cape of Good Hope ("Challenger"), 89.4.24.1; one from S. Africa, 1907.8.29.27; one from Venezuela; one from the Philippine Islands, 1903.7.4.1; one from Tahiti (M.C.); one from the Loo Choo Islands; one from the Sandwich Islands (M.C.); thirteen from unknown localities.

(*b*) In M.H.N., Paris. Twelve from the Mediterranean; one from Guadeloupe; one from Île de France; one from Java and two from unknown localities.

(*c*) In Mus. Oc. Monaco. Two from Monaco

*Distribution.*—Mediterranean (Carus, Auctt.); Madeira (Hoyle); Azores (Joubin, beach); Portugal (Joubin); New Jersey (Lockwood); Martha's Vineyard—Newport, R.I. &c. (Verrill (64–365 fms.); Florida (Anon.); "W. Indies" (Rang, *fide* Orbigny); Cuba (*id.*, Molina); Venezuela (B.M.); Cape of Good Hope (Orbigny, Auctt.); Cape Agulhas (B.M.); Simon's Bay (B.M.); Red Sea (Orbigny, Wülker); Amboina (Rumphius, etc.); Tahiti (B.M.); Sandwich Is. (B.M.); Loo Choo Is. (Lischke, B.M.); Japan (summary in Sasaki, 1929); Cocos Id., E. Pacific, surface (Hoyle); Cape San Francisco, Colombia (*id.*); L. California and Panama (Tryon, Dall); New Zealand (Kirk); Australia (Brazier).

The status of many forms being doubtful, it is naturally uncertain if the world-wide distribution given above is correct. The British Museum specimens from Venezuela, Tahiti and the Sandwich Is. are undoubtedly

referable to *argo*. Verrill says that the N.E. American forms " belong to the common Mediterranean variety," and Suter's description of the New Zealand specimens seems to tally with *argo*. Sasaki (*l.c.*, p. 23), on the other hand, is plainly uncertain as to the Japanese examples, though the shells figured (Pl. III, figs. 8–12) leave very little doubt in the mind. For Dall's *pacifica* see p. 180. The species actually seems to occur in most tropical and subtropical waters. A living specimen and fresh shells have been taken as far north as Rhode Island in N.E. America, though there is no record farther north than Portugal on the eastern side of the Atlantic.

Curiously enough, I can find no records from the N. Indian Ocean. Hornell, Massy, Winckworth, Brock, Goodrich, Ortmann, Hoyle (Manaar, Laccadives and Maldives) all fail to record it. I am also indebted to Mr. R. Winckworth for informing me that he has no record of *A. argo* among the Indian and Singhalese observations. As far as I can see there are likewise no records from South America south of the Equator (? Jatta, 1889).

Sasaki (1929, p. 23) says that he refers the Japanese specimens seen by him to *argo* " with a great deal of hesitation." He says (*l.c.*, p. 25) that they differ from the Mediterranean form, as described by Jatta, in the following particulars : (1) the outer laterals are shorter and " only slightly longer or even shorter than either the internal lateral or the median teeth." Jatta certainly shows the second and third laterals as much larger than the admedian and median. Naef does likewise, though perhaps less markedly than Jatta. In my preparation of Mediterranean *argo* I do not find this disparity. The second and third laterals are about equal in length and only a little longer than the admedian and median. (2) The Japanese form is said to have one or two faint cusps at the base of the median which are not given in Jatta's figure. Such cusps are absent in my specimen, but are shown by Naef. (3) The funnel-organ is said to be composed of thicker pads of which the ventral ones are a little longer than those seen in the Mediterranean form. This seems to be a fairly constant, though unimportant, difference. The arms of the Japanese specimen measured by Sasaki seem rather longer than is usual in the Western forms.

The shell and other features seem to differ in such slight respects that I am loth, in spite of the points just discussed, to doubt the accuracy of the earlier diagnoses of Japanese *argo*.

*Description.*—(A) *The female.*—The mantle-sac is narrowly or broadly ovoid, shaped usually, as Jatta says, like a Phrygian cap. There is usually a wide and blunt apical point. The head is relatively small and rather sunk into the mantle. The eyes are prominent. The mantle-aperture is very wide and is actually continued past the eyes in a dorsal direction. The ventral edge is much thickened. The arms differ in the order of size. Jatta gives the latter as 4.2.1.3, Sasaki and Naef as 1.4.2.3, while in our British Museum specimens I find 1423, 4213 and 4123. I think that the first arm must exhibit seasonal- or age-variation. The first arms are thicker than the others at the base. They bear the characteristic membrane which extends nearly the whole length of the arm (Naef, fig. p. 775) or 61–74% of it (B.M.). The membrane is figured in detail by Naef. In his paper it is shown as about 9 times as wide as the arm at its broadest. The arm is bent twice on itself, the proximal bend

being gradual, the distal more abrupt. The second bend brings the distal section of the arm to lie more or less parallel to the basal moiety. The arm then comes to enclose its membrane and the last section exhibits a glandular thickening on its inner side which constitutes the area of shell-secretion. The suckers are closely alternating and normal basally, though they are rather small and the basal cup is relatively shallow. The distal suckers become very minute. The other arms do not call for special description. They taper very gradually to very slender extremities. The fourth pair is provided with a high dorsal keel which is more prominent proximally. The bases of the arms are joined by a very low web. This is deepest in sector A, but even so it is only 8% of the 1st arms. That of Sector B is usually next in depth, D next, C and E being subequal and smaller still.

Jatta thus describes the colour of the living animal—"grigio perla con una sfumatura azzurra la quale è più accentuata sopra le braccia." He

Fig. 26.—*Argonauta argo* (♀). Pallial and siphonal elements of the adhesive-apparatus.

does not allude to the chromatophores known to characterize the animal by earlier writers (Sangiovanni, Vérany). The chromatophores are found fairly densely on the dorsal surface of the mantle and head and on the first 2 pairs of arms. They are less prominent on the 3rd and 4th pairs, though there is a fair scattering round the base. The ventral surfaces are free of them. There is a powdering of fine ones on the dorsum and all round the end of the funnel.

The mantle is articulated to the siphuncular region of the head-foot by an adhesive organ, similar in principle to that seen in the Decapoda, but differing in one respect (Text-fig. 26). The pallial element is a roundish knob at the base of which is a narrow transverse depression. The knob fits into a deep and appropriately-shaped cephalic element, the inferior lip of which is flanged so as to fit into the negative pallial element.

The funnel is very long. It projects beyond the eyes and its aperture actually lies in advance of the edge of the ventral sector of the web. Its base is widely arcuate. The funnel-organ is \ Λ /-shaped, the limbs being all slender and pointed.

*Pallial cavity.*—The adductor pallii medianus is small and its attachment to the visceral sac is very slight. The gills are rather elongated and have up to 13 filaments aside.

*Alimentary tract.*—The pharyngeal mass has been described by Heinrich (1904). There is an outer tuberculous lip and an inner thin one. The upper jaw is rather weak as compared with that of an *Octopus*, the beak being small and the anterior edges little modified; the rostral lamella is deep (two-thirds of the palatal) and the whole jaw is wide. The beak of the lower jaw is also small and the anterior edges of the rostral lamella unmodified. The jaws are only feebly chitinized.

*The radula.*—The central teeth are unicusped with a tall, slender mesocone. The admedians are almost as tall and slender with a small base. The second laterals have a long and more solid cusp, and a longish base (longer in specimens seen by me than is shown by Jatta). The third laterals are slender and gently curved. The marginal plates are narrow. There are two pairs of salivary glands, of which the posterior (unlike those of the Octopodidae) are smaller than the anterior. The crop is not a separate dilatation of the oesophagus, but a more or less swollen part of the latter. The stomach is rather thin-walled and the massive grinding mechanism seen in other forms is ill-developed. The coecum, liver and intestine call for no comment. The ink-sac is more or less imbedded in the liver. Pelseneer in an ambiguous passage (1906, p. 303) seems to suggest that it is free. This may be due to a rather diagrammatic figure of Poli's, in which the ink-sac is shown quite free. I have dissected four specimens and in each I find the sac is sunk into the liver, but quite superficially (cf. *Pteroctopus*, Robson (1929, fig. 5)).

*Reproductive organs.*—These have been figured by Brock (1882, Pl. xxxiv, fig. 6). The distal oviducts are long and slender, apparently without any vaginal swelling. There is a moderately-sized oviducal gland and the proximal oviduct is very short.

The nervous system has been figured by Pfefferkorn (1915).

*The shell.*—The largest specimen I have seen measures $11\frac{1}{4}$ in. over all. Gould (in Tryon, *l.c.*, p. 136) records one of $11\frac{3}{4}$ in. (? actually 10 in.).

The shell is compressed, with a narrow keel rarely exceeding 6% of the aperture length in specimens over 200 mm. in diameter. The aperture (p. 178) is more usually narrow, but may be wide, and its sides are either gently rounded with the convexity outwards or angled in the columellar region, the angle forming a projection which may be bent outwards into a prominent " ear " or towards the columella.

The keel has a double row of low but usually sharp tubercles. The surface is traversed by a number of ribs, which may be simple and stretch from the columella to the carinal tubercles in which they terminate, or bifurcate in various ways. Lastly, the smaller parts of the bifurcation may become detached so as to become secondary ribs. The colour is a glistening white, the keels being brown or blackish.

(B) *The male.*—Naef (*l.c.*, p. 787) says that the largest specimens of male (including the arms, but not the hectocotylus) he obtained never exceeded 15 mm. The largest Mediterranean female specimen which I know, is one in the British Museum, which is 310 mm. over all, or 20 times as large as the male. I do not know if the Indo-Pacific males are larger than Naef's.

The body is of a rounded-conical shape. The head is relatively large and the eyes of a considerable size, though they are scarcely prominent. The arms, according to Naef (*l.c.*, p. 786), are in the order 1, 4, 2, 3, though they are little different in size. They carry some 12 suckers each, of which the 3rd–6th are very large and the distal ones very minute. The arms might be considered to be 50% or slightly less of the total length. They are joined for about $\frac{1}{2}$–$\frac{1}{3}$ of their total length by a web, which seems to be deepest in Sector C.

The funnel is not so large as in the female, though it extends beyond the eyes. According to Jatta the funnel-organ is like that of the female.

The body is covered ( ? equally) with brown and gold chromatophores, the skin having otherwise a blue and violet sheen, especially on the dorsum and eyes (Naef).

The adductor pallii medianus is relatively larger than in the adult female. The other pallial organs are like those of the female.

*Genitalia* (Marchand, 1907, p. 377).—The penis has a large (anterior) diverticle and a small appendix ( ?). The accessory gland is small and Needham's organ of the ordinary size. The vas deferens is subdivided into three spermiducal glands. The proximal part of the vas deferens begins with a large oval " ampulla."

*The hectocotylus.*—The third arm on the left side is transformed into the well-known autotomous hectocotylus.

When undischarged this organ is contained in a sac formed at a very early developmental stage around the arm tip, which becomes bent on itself. In addition, according to Grimpe (1928, p. 94), the hectocotylus-sac " aus den Schirmhautverbindungen zwischen Hectocotylus und Ventral-, bzw. Laterodorsalarm hervorgeht."

When fully expanded the hectocotylus is seen to consist of (*a*) a basal spermatophore reservoir, (*b*) a sucker-bearing part, flattish in section and carrying as many as 95 suckers which are mainly directed sideways, (*c*) (beyond *b*) a long and slender lash-like penis, which usually exhibits a basal triangular appendix ( ?).

*Variation.*—Von Martens (*l.c.*), Dall (*l.c.*) and others have commented on the variability of the shell in this and other Argonaut species. The " phases " or " forms " which von Martens recognized have been already described and discussed (p. 178).

*Habits.*—Very many references to the habits of *Argonauta argo* are to be found in the literature. The early ones invariably allude to the wholly fanciful story concerning the use of the arms, to which reference is hardly necessary. From zoology these references found their way in various forms into general literature, and our poetry has been enriched with many similes derived from this source. Christina Rossetti's " rainbow shell that paddles in a halcyon sea " is obviously an echo of the persistent story of the Argonaut's use of its arms as paddles. Reference is hardly necessary to the long controversy as to the rôle of the hectocotylus.

The Paper Nautilus seems to be an inhabitant of warm and temperate seas (see p. 185 for peculiarity of its known distribution). It is found most often at the surface, though Verrill records it from greater depths.

Like the rest of the group, *A. argo* is carnivorous and feeds on Crustacea (Lo Bianco) and Fish (Lacaze Duthiers). It seems to spend its time

swimming slowly about with the body all but completely submerged. Rang and others state that it swims at some distance below the surface.

Lacaze Duthiers (*l.c.*) found that it lived for 15 days in captivity. The general verdict seems to be that it does not survive in aquaria. Lacaze Duthiers (*l.c.*, p. 42) makes an interesting comparison between this animal and other cephalopods. He notes that the expression of the eyes of the Octopus and Cuttlefish is "une expression profondement intelligente et canaille." Even at rest they are watchful and alert. The Argonaut, however, is quite impassive. The eye is expressionless and no excitement seems to change its expression.

*Reproduction.*—Lo Bianco (1909, p. 645) obtained eggs and embryos in various stages in May–October. Young specimens (10–15 mm. long) are taken on the surface in September–November. The eggs are like those of *Octopus vulgaris* in shape and colour. They are, however, of smaller size (Naef, 1928, p. 71, gives the average dimensions as ·6 × ·8 mm.). Naef gives an account of what is known of the development, and Grimpe (1928, p. 77) has described early stages of the male.

The marked sexual dimorphism in size and structure has been already fully described. So far as I can find, no author has any certain views as to the habits of the male. It seems to me inconceivable that in a pelagic species the dwarf male with its cumbrous hectocotylus should be anything else than symbiotic with the female. Naef (1923, p. 784) is apparently of this view, though he apparently has no definite information on the subject. As Grimpe says (*l.c.*, p. 79), practically nothing is known about the mating habits of these animals; the only certain piece of information is that occasionally mature males are found in the shell of the female, and that several fresh hectocotyli may be found in the female mantle cavity.

Lacaze Duthiers (*l.c.*) and Naef (*l.c.*) describe the rôle of the dorsal arms in carrying the shell. Apparently the membrane of the arms is spread over the outer surface of the shell and the latter is grasped by the suckers of the arms along the row of carinal tubercles. The membrane can, however, be withdrawn and the arm thrust inside the shell. During this change of position the suckers keep a hold on the shell (cf. Naef's fig. 465). It seems quite clear that the shell can be readily abandoned, and this seems to be done regularly by the animal when in ill-health. But it can be also made to drop the shell by force, after which, however, it seems to pick it up again and get it into position (Naef, *l.c.*, p. 775, footnote).

*Discussion.*—Linné's description is very brief ("carina subdentata") and quite useless as a clue to the identity of this species. He cites eight authors, and it is enough to say that the figures quoted indicate several species (*e.g.* those of Rumphius, *l.c.*, Pl. xviii, B) and Gualtieri (*l.c.*, Pl. 12, 271, C). Gmelin (*l.c.*), who followed Linné, did not distinguish the species more clearly He quoted a larger array of authors with the same medley of forms. His description is longer, but adds nothing definite. The ribs are "levibus vel nodulosis" and the keel is "utplurimum fuscescente." I do not think any genuine *argo* is nodose (see Variation, p. 179), and the keel is dark in other forms (*hians*, *gruneri*, B.M.). The credit for the first attempt to regularize the position of this form is due to Schröter (1783), who regarded it as a very variable form sometimes with auricles and with simple, nodose or forked ribs. His language is strangely modern

" daraus ist deutlich dass der Pappiernautilus in verschiedenen Abänderungen vorkomme . . ." (*l.c.*, pp. 4–5). Bruguière (1792) took the same view and sets forth the variants in a more exhaustive fashion. It should be noted that Schröter (*l.c.*, fig. 1) takes as his figure (and we may assume as the typical form of *argo*, Linn.) the simple-ribbed, narrow-keeled form (as far as we can judge) without auricles. To whom the credit of fixing the identity of the Linnean species is due is, I think, quite fruitless to decide. Dall (1908, p. 227) has attempted to secure this for the ambiguous Bolten (1798). Bolten certainly (*l.c.*, p. 70) alludes to *A. Argo* (no author) as the " Schmalkieligte Papier-Nautilus," and he cites Martini's (1769) fig. 157, which is that of an *argo* in the modern sense. But he also cites the unfortunate mélange of Gmelin (see above), so that he cannot according to strict criteria be taken as having defined Linné's species. It would, I think, be quite valueless to probe the matter author by author and decide exactly how much each contributed to a clarification of the position. The truth is that, with a form like *A. argo*, an exact knowledge of the identity of the species grows almost imperceptibly, and the purging from it of foreign elements goes on slowly. I may even point out that Hanley as late as 1855 does not really clear up the situation. After pointing out (p. 153) that in the synonymy of the " Systema " and the " Museum Ulricae " three species are confused, he merely says that *A. tuberculosa* and *A. nitida* " are confused with *that shell for which the name Argo has more especially been reserved by cochologists.*" He cites the Mus. Ulricae description, of which the phrases " anfractus transversim undulato-plicati, carinati serie duplici aculeorum brevissimorum " are the most important, but does not fix our *argo* of modern usage, because the width of the keel is not mentioned. He does say, however, that a specimen corresponding to Sowerby's *argo* (1831, Pl. 277) is in the Linnean cabinet, though as Linné had quoted a heterogeneous assemblage in 1758, this can hardly be held to prove that he had any definite form in mind. The Museum Ulricae quotation shows a growing appreciation of the need for clarity, but is not final. I think it would be safe to say that by the middle of the 19th century the name *argo* was regularly given to the flattish form with narrow carina composed of two series of low teeth and simple or bifurcate (not knobbed) ribs. The conviction that it is polymorphic, however, contributed to keep its precise definition in doubt. This idea started by Schröter and followed up by Bruguière was adopted by Orbigny (1840), by von Martens (*l.c.*) and Dall (*l.c.*). Von Martens (*l.c.*, p. 104), as we have seen (*supra*, p. 178), distinguished three " forms " according to the shape of the edge of the aperture. As far as *argo* is concerned, he distributed the described specimens into one or another of these " forms." Dall (*l.c.*, p. 225) is less categorical, but he seems to be of the same general opinion. " It is also practically certain that in this (*argo*) and the *hians* groups the presence or absence of auriculation is not a specific character. Some species appear to be always auriculate, others always without these projections, while others again have an auriculate and a simple form with intermediate gradations occasionally." There is some uncertainty as to the meaning of " auriculation " (see p. 178), and neither von Martens nor Dall noted that, in addition to the variation in the shape of the aperture when seen *en face*, the degree to which the edge is angulate when viewed laterally varies

very much. In some forms the auriculate form occurs in the Mediterranean (Dall says inaccurately that moderate auriculation is the rule in Mediterranean specimens, *l.c.*, pp. 227–28), cp. Jatta (*l.c.*, Pl. 18, figs. 25*a*, *b*, *c*) and B.M. ("Piedimonte"). The significance of the variation is discussed on p. 178. It is enough here to say that the presence of these variant stages has contributed to the uncertainty as to the exact definition of *argo* and also as to the forms which should be regarded as synonyms.

However that may be, the shell of *argo* is, in the light of more study on its variation, seen to be characterized by two steadily correlated characters, a narrow keel with low knobs and continuous (smooth) ribbing.

It remains to discuss a few of the more important synonyms.

1. *A. Pacifica*, Dall (1869, p. 238); "*A. argo*, Cooper, not Linné," Dall (1871, p. 95, where?); *A. Pacifica*, Dall (*l.c.*); *A. pacifica, id.* (1908, p. 225); *A. argo pacifica, id.* (*l.c.*, p. 226).

Dall did not properly describe the shell in any publication known to me. The first allusion in 1869 (cited as the first by Dall himself, 1871, p. 95) to it simply says "I proposed the name *pacifica*" (where?), and the three subsequent allusions give no other clue to its identity than the citation of a figure from Reeve. However, Dall describes the external parts and radula, which he describes as differing in some respects from *A. argo*.

Dall's later treatment (1908) is a little muddled. On p. 225 he calls it *A. pacifica*, treating it as a distinct species with evident doubt. On p. 226 it is *A. argo pacifica*! On p. 228 it is alluded to as *A. pacifica*, Dall, without discussion of the status.

The only characters mentioned (1908, p. 225) are that it is "rounder, wider and shorter" than those from the Mediterranean. I do not think that these differences stand for much, nor am I satisfied that the figure of Reeve cited by Dall shows any substantial varietal difference from *argo*. The characters of the arm and web seem to be unimportant, and the radula requires illustration before we can seize its peculiarities. I think it better to keep this form as of "uncertain status," though I am prepared to believe that the Californian form may be on closer examination a variety of *argo*.

2. "*A. argo* var. *mediterranea*," Monterosato (1913). Monterosato distinguishes this from the typical *argo* by its shell, which is less thick and its more numerous ribs. I do not think a varietal status is indicated on the above characters. The form (Pl. X, fig. 2) is rather unusually deep.
3. "*Argonauta cygnus*," Monterosato (1889, p. 120). "Plus comprimé que les autres, ses rugosités sont nombreuses et ses crochets très obtus même à l'état jeune *id* (1913)." The figure given by Monterosato (1913, Pl. XI, fig. 2) shows a "mutica" form, but otherwise characteristic.
4. "*Argonauta monterosatoi*," Coen (*l.c.*). A form with a widely obtuse angle on the lip when seen laterally. The ribs are few in number, but the form is otherwise normal. Japan and Adriatic.
5. "*Argonauta Ferussacii*," Monterosato (*l.c.*, as of Valenciennes MSS.). "L'ouverture très dilatée, rugosités très nombreuses et encore plus rapprochés que chez l'*A. cygnus*." This and *A. Sebae* (*l.c.*) seem to be undeserving of varietal status.

**Argonauta hians,** Solander.

*Nautilus* . . . , Lister (1688, tab. 554–5*a*).
*Nautilus minor*, Rumphius (1705, p. 64, Pl. 18, fig. B). (?) " eine feinere Sorte des papiernen Nautilus," *id.* (Edn. 1766, Pl. 18, fig. 4).
*Cymbium* . . . , Gualtieri (1742, t. 12, CC).
*Nautilus* . . . , Argenville (1742, p. 250, Pl. 8, fig. 1 B; Ed. 1757, p. 198, Pl. 5, fig. B).
*Nautilus* . . . , Hebenstreit (1743, p. 297).
*Nautilus sulcatus* (? pars), Klein (1753, p. 3, sp. II).
(?) *Nautilus tenuis* et *legitimus*, Knorr (1757, tom. 1, tab. II, fig. 2; tom. IV, tab. XI, fig. 1).
*Nautilus tenuis*, Seba (1758, t. LXXXIV, figs. 9–11).
*Argonauta argo*, Linné (1758, p. 708, No. 231, *pars*).
*Nautilus tenuis minor*, Petiver (1764, tab. 10, fig. 2; tab. 22, fig. 10).
*Nautile papyracé* . . . , Meuschen (1767, p. 10, Nos. 66–67).
(*?*) *Nautile* . . . , Davila (1767, p. 108, No. 87, 2nd species).
(?) *Nautilus tenuis* . . . , Martini (1769, p. 235, t. XVII, figs. 158, 159).
*Argonauta argo*, Murray (1771, p. 36, tab. 1, fig. 8).
" *Nautile papyracé à stries rares*," d'Herbigny (1775, tom. II, p. 426).
" Papier brouillard, Nautile uni," etc., Favanne (1780, t. 1, p. 711, Pl. VII, fig. A 6; p. 713, figs. A 10, A 1; p. 717, fig. A 5).
*Argonauta argo*, var. b, Born (1780, p. 140).
,, *rugis* . . . *crassis* (*?*), Gronovius (1781, p. 281, No. 1215).
" Papier nautilus," Schroeter (1782, p. 51, No. 272, tav. XL, fig. 272).
" papier Nautilus, var. *β*," Kaemmerer (1786, p. 29).
*Argonauta hians*, Solander (1786, p. 44).
(?) ,, *navicula*, *id.* (*l.c.*).
*Nautilus legitimus*, Geve ((?) 1790, p. 14, t. 2, figs. 6, 7; *id.* (2nd edition) p. 8, t. 2, figs. 6–7)).
*Argonauta argo*, var. d, Gmelin (1790, p. 3368).
,, ,, ,, c, Bruguière (1792, t. 1, p. 123).
,, *hians*, Humphreys (1797, p. 6, No. 82).
"Argonauta papier brouillard croissant (*?*)," Montfort (1802, pp. 358, 371).
*Argonauta argo*, var. 3, Turton (1802, t. IV).
,, *hians* and (*?*) *gondola*, ? *haustrum*, Dillwyn (1817, pp. 334, 335).
(?) *Ocythoë cranchii*, Leach (1817, p. 296, Pl. XII, figs. 1–6).
(?) *Argonauta raricostata*, *id.* (*l.c.*, Pl. XI) [*fide* Orbigny].
(?) *Ocythoë cranchii*, *id.* (1817*a*, p. 139).
,, ,, *id.* (1818, p. 394).
*Argonauta hians* etc., Wood (1818, p. 62, No. 3).
*Ocythoë cranchii*, Tuckey (1818, p. 400, No. 11).
" Ocythoe de Cranch," Blainville (1818, p. 456, Pl. Juin 1818, fig. 2, A, B).
,, ,, ,, *id.* (1819, p. 49).
*Ocythoë cranchii*, Oken (1819, pp. 255, 257, Pl. 3, figs. 1–6).
*Argonauta nitida*, Lamarck (1822, p. 653).
,, *hians* etc., Férussac (1822, p. 553).
(?) ,, ,, Orbigny (1826*a*, p. 48).
,, *Hians*, *id.* (1826, p. 138).
(?) ,, *nitida*, *raricosta*, *crassicosta*, Blainville (1826, p. 213).

*Argonauta nitida*, Crouch (1826, p. 43, Pl. XX, fig. 17).
" Poulpe de Cranch," Blainville (1826 (?), Pl. 6, figs. 2 and 2*a* [cited as I *bis* by Orbigny]).
*Argonauta raricostata*, Deshayes (1830, p. 69, No. 1).
,, *hians*, Orbigny (1840, p. 174, Pl. 5).
*Ocythoë cranchii* and *Argonauta hyans* [sic], Gray (1849, p. 33).
*Argonauta owenii*, Adams and Reeve (1850, p. 4, Pl. 3, figs. 1*a–d*).
,, *gondola*, *hians*, *id.* (*l.c.*, pp. 3–4, Pl. 3, figs. 2*a–c*).
,, *Kochiana*, Dunker (1852, p. 49).
,, *polita*, Conrad (1854, p. 333, Pl. 34, fig. 4).
,, *Kochianus* [sic], Dunker (1865, p. 29, Pl. 9, figs. 7–8).
,, *gondola*, Reeve (1861, Pl. IV, 3*a* and 3*b*), *hians id.* (*l.c.*, Pl. IV, fig. 4), *oweni*, *id.* (*l.c.*, Pl. IV, fig. 5).
,, *hians*, von Martens (1867, p. 105).
,, *gondola*, Lischke (1869, p. 29).
,, *hians*, Molina (1878, p. 147).
,, ,, Tryon (1879, pp. 133, 136, Pl. 46).
,, *Owenii* and *gondola*, Dunker (1882, p. 1).
,, *hians*, Ortmann (1888, p. 641).
(?) *Argonauta argo*, var. *americana*, Dall (1889, p. 174, Pl. 67, figs. 1–3).
*Argonauta hians*, Brazier (1892, p. 2).
,, ,, Hoyle (1904, p. 11).
,, ,, and *gondola* Hidalgo (1904, p. 9).
,, ,, (vars. *hians* and *navicula*) Dall (1908, pp. 226, 229).
(?) *Argonauta navicula*, Berry (1912, p. 385).
*Argonauta hians*, Chun (1915, p. 476, Pl. LXXIV).
,, ,, Sasaki (1920, p. 171).
,, ,, *id.* (1929, p. 20, Pls. III, VIII, text-fig. 6).

[One or two early works cited by Orbigny (1840) in his Bibliography have not been traced.]

*Type.*—Not traced.

*Specimens seen.*—(*a*) In British Museum.

i. *Complete specimens.* One from Misaki (Japan) (1921.12.20.203); three from Masqat; three from unknown locality.

ii. *Shells.* Twenty-one from the Philippine Is. (10 M.C.) (one the figured " Samarang " specimen); four from the Moluccas (2 M.C.); four from the Persian Gulf (including 68.1.1.20); two from " China " (M.C.); one (abnormal) from Albay, Luzon (M.C.); thirteen from unknown locality.

(*b*) In M.H.N., Paris.

A series of auriculate specimens, ? loc. (" *A. nitida* "); one from New Guinea.

*Distribution.*—Found almost everywhere in tropical and subtropical waters. The following list of occurrences may be noted :—Japan (Brit. Mus., Ortmann, Lischke, Sasaki, Dunker), China (Dunker, 1865), E. America to 43° N. (Dall), Moluccas (von Martens, Brit. Mus.), Philippines (Brit. Mus., Hidalgo), Red Sea, Masqat (Brit. Mus.), N. Pacific 21° 19′ N., 106° 24′ W. (?) in 680 fms. (Hoyle), off Cape Palmas, W. Africa (" Valdivia " Stn. 50, Chun) Bourbon, New Guinea, Amboina, Teneriffe, Rio de la Plata, S. Ocean, Valparaiso (Orbigny), Coast of Africa (Gray), Queensland (Brazier).

*Description.*—The following description is based on those of Orbigny

and Sasaki (♀). Chun's specimens are too immature and those in the British Museum are in too poor condition to be of much use. The body is oval or conical, and its width is less than its length (Sasaki), perhaps wider (Orbigny gives the length as 12 mm. and the width as 14 mm.). The head is small and the eyes prominent. The arms are in the order 1.2.3.4 (Sasaki), 2.3 = 4.1 (Orbigny, young), and 66–54 of the total length. The suckers number 80 on the second arms of an immature specimen. Sasaki found 60 pairs on the first arms. He notes that on the 2–4th arms the second or third pair is the largest. The brachial membrane of the first arms seems is be normal. The web is " very narrow : longest radius between dorsal arms about twice those between other arms." The funnel is very long according to Sasaki, and extends nearly one-third up the ventral arms. In Orbigny's figure it seems to be rather longer. There are 10 filaments aside in each demibranch. The funnel-organ (Sasaki) is \/\/ shaped. The locking apparatus is small but well developed on the siphonal side. It is ovate in shape and transversely arranged. The pallial element consists of a rounded nodule " with the extremity directed posteriad." The female genitalia (immature specimen, Sasaki, text-fig. 6) exhibit very short proximal oviducts and very small spermoviducal glands. The distal oviduct is long and fairly stout, and terminates in globular expansions.

The hectocotylus (Sasaki) is not unlike that of *A. böttgeri* figured by Berry (p. 196). The sucker-bearing part is 15 mm. long and narrows down gradually towards the distal end. The distal part (filament or penis) is a little longer than the proximal part. There are 45–50 suckers in all. They are connected by a membrane which is " as broad as the suckers are high."

The shell in its most characteristic phase is characterized as follows. The surface is finely granular, though the granules may get worn off. There are about 32 moderately prominent ribs, about half of which are complete, the smaller ones being more or less regularly intercalated between complete ones, there being about two ribs to each carinal knob. Auriculate and inauriculate forms are found, both among old and young specimens. The interauricular width may be very considerable, the maximum I have obtained being 76% of the total length. The keel is very clearly marked, and its width may be 24% of the total length. The carinal knobs are very prominent and more or less triangular. There are 15–23 in each row in adult shells. Usually they are nearly all a deep rich brown in colour, and the angles of the keel may be shaded in brown with the median part white. The general surface is fawn or white.

The most marked variant on this form is the variety recognized as *navicula* by Dall. This is Solander's *A. navicula* (founded on Rumphius' figure 4, Pl. XVIII), and is characterized by a greater number of ribs (up to 42) and knobs (over 30). There seems to be a gradation from the extreme phase exemplified by *navicula* to *böttgeri* (*q.v.*), and certain specimens are not easy to diagnose. I have, on the other hand, found no intermediate forms between *hians* and *nodosa*. The largest shell that I have seen is *c.* 108 mm. long (Brit. Mus.).

*Habits.*—According to Orbigny (*l.c.*, p. 176) the animal is nocturnal and gregarious.

*Remarks.*—The shell is very distinctive in its extreme phase, which

occurs frequently enough to justify its treatment as a separate species. It is closely related to *böttgeri*; but I agree with Dall that the two forms are distinct. Dillwyn's enigmatic *haustrum* is provisionally treated as a synonym.

**Argonauta böttgeri,** Maltzan (? = **hians,** var.).

*Argonauta Böttgeri*, Maltzan (1881, p. 163, Pl. VI, fig. 7).
? „ *oweni*, Dunker (1882, p. 1).
„ *Böttgeri*, Smith (1887, p. 409, Pl. XVII, figs. 1–6).
? „ *oweni*, Ikeda (1891, p. 27).
„ *Böttgeri*, Hidalgo (1904, p. 161).
„ *böttgeri*, Dall (1908, pp. 226, 229).
„ „ Berry (1909, p. 418).
„ „ „ (1914, p. 277, Pl. XLVIII, fig. 5, text-figs. 3–7).
? „ *hians navicula*, Berry (1912, p. 385).
„ *böttgeri*, Massy (1916, p. 143, text-figs. 1–2).
„ „ „ (1916*a*, p. 188).
„ „ Sasaki (1920, p. 171).
„ „ „ (1929, p. 22, Pl. III, fig. 7; VIII, fig. 11).

*Type.*—Not traced.

*Specimens seen.*—In British Museum.

(a) *Shells.* One from Albay, Luzon (M. Cuming); two from Japan (1915.1.4.198–199); two from Mauritius (Robillard, 85.9.19.30–31); two from " Australia " (M.C.); three from Masbate, Philippines (M.C.).

(b) *Complete specimens.* Two from near Chagos Id., Indian Ocean (Keane); one from " China Seas " (87.11.14.1); one from Three Kings Id., New Zealand (" Terra Nova ").

*Distribution.*—" Australia," Masbate etc. (Philippines), Mauritius, " China Seas," Chagos Id. (Indian Ocean) (Smith); ? Philippines (Hidalgo); between Honolulu and Laysan Id. (Berry) (surface); New Zealand (Massy); Japan (Dunker, Sasaki (700–750 fms., 1920), Ikeda); Andaman Is. (Massy).

*Description* (♀ only).—The complete specimens in the British Museum are not in a good enough condition to justify my using them for this description, which is largely founded on those of Berry, Massy (1916) and Sasaki. Massy's Andaman Islands specimen (*ead.* 1916*a*) seems to have been in poor condition, so I refrain from using her measurements.

The body is cylindrical, twice as long as broad (Berry), or as broad as long (Massy, 1916). The head is as wide as the body, but it is small in size. The eyes are large and prominent. The arms are in the order 1.2.3.4 (Berry) or 2.4 = 3.1 (Massy 1916*a*). It is possible to calculate the length of the arms only in Berry's specimen, in which they are 61% of the total length. The expanded membrane of the first arms is normal; the web between the other arms very shallow (extending on all arms to about 3 mm. from the base (Berry), or to the third sucker laterally and about the fourth dorsally and ventrally (Massy). The suckers are large and much elevated (6–12%). In Massy's specimen the apex of the funnel reached to the level of the mouth. In Berry's it is longer. The funnel-organ is \ /\ / -shaped. Smith described the jaw of his specimen as " coal black." In both mandibles the rostrum was remarkably small.

The radula as figured by Smith is very unlike that shown by Massy, and I herewith tabulate the chief differences :—

| | Rhachis. | 1st lateral. | 2nd lateral. |
|---|---|---|---|
| Smith | tricuspid | equilateral, narrow base | more or less equilateral |
| Massy | tricuspid | asymmetrical, wide base | asymmetrical |

There seem to be 11 filaments in each demibranch.

The *hectocotylus* (Berry, *l.c.*, p. 279) consists of a thick curved basal part about 6 mm. long, carrying two rows of about 22 suckers connected by a delicate membrane. The "outer aspect" is keeled and bears a conspicuous marginal membrane. Distally the organ is continued as a long and thread-like "flagellum" (penis), 13 mm. in length. The eggs do not seem to exceed 1 mm. in length.

*The shell.*—The colour tends to be of a pale buffish brown, but completely white forms are known. The keel is described by Sasaki as having "its width at the ventral margin of aperture equalling a half of the shell-width." Berry and Smith do not mention the width. I obtain the following dimensions :—

| | Length of shell. | Width of keel. |
|---|---|---|
| 1. | 51 mm. | 12 mm. |
| 2. | 49 ,, | 8 ,, |
| 3. | 34 ,, | 7 ,, |
| 4. | 33 ,, | 6 ,, |
| 5. | 31 ,, | 5·5 ,, |

The keel is well defined and devoid of ribs. Its knobs are rather blunt but prominent ("very prominent" (Sasaki)). They are recorded as follows :—Sasaki, 18–19 (full-sized specimens); Berry, 17–18; B.M. (Smith) and type, 33–14; B.M. (Robson), 20–22. The difference between Sasaki's full-sized specimens (of 58 mm.) with 18–19 and Smith's large Philippine specimen (40 mm.) with 33 is very notable. The tubercles do not seem to be dark. The ribs are as follows :—Sasaki (58 mm.) 45 +; Berry (? size), 30 +; B.M. (51–49), 35–37. They are very prominent. They are sometimes branched and in many specimens there is a rough tendency for incomplete ribs to be intercalated between the complete ones. The surface is finely granular in places. I have found no auriculate specimens, and Berry and Dall evidently regard the species as inauriculate. Sasaki, however, says "the auricles are invariably inconspicuous" (? present). The aperture is usually wide, and in one specimen (Luzon) I found it to be half the total length of the shell.

*Remarks.*—The relation between the various specimens that have been described is very uncertain. Certainly the radulae figured by Smith and Massy do not seem to come from the same species. The number of tubercles and ribs varies very much.

Sasaki says that this species is closely related to *A. hians* "especially

in the soft parts," and states that the only difference is that in our species the arms are a little longer and the suckers somewhat larger. The largest specimen recorded seems to be Sasaki's No. 1 (58 mm.). The species is thus somewhat small and might be regarded as the young stage of *hians*. However, at all stages down to *c.* 25 mm. the shell can be distinguished by its more numerous ribs and tubercles, by the lack of auricles, by its regularly granular surface, and finally by the almost invariable absence of colouring on the carinal knobs. In spite of this quite tangible difference, I think the species is very closely related to the form *navicula* of *hians*, and to the ambiguous *cornuta*, and one or two examples in the British Museum are very hard to assign to one or the other form. An instance of this is an inauriculate specimen from Goram Island in the British Museum (1910.6.18.47), with 23 dark carinal knobs, 36 (?) ribs, no granules on surface. It measures 70 mm. over-all.

**Argonauta cornuta,** Conrad.

? *Nautilus tenuis*, Rumphius (1705, Pl. XVIII, fig. 4).
*Argonauta cornuta*, Conrad (1854, p. 332, Pl. XXXIV, fig. 2).
? ,, *dispar*, Conrad (*l.c.*, p. 332, Pl. XXXIV, fig. 3).
,, *expansa*, Dall (1873, p. 303).
,, *Owenii* (? var.), Tryon (1879, p. 137, figs. 104–105); *expansa*, Dall (1902, p. 511, Pl. 33, figs. 1, 2, 3).
,, *cornuta*, Dall (1908, p. 224).

*Type.*—Coll. Acad. Nat. Sci. Philadelphia and J. S. Philipps (syntypes).

*Distribution.*—Gulf of California, Gulf of Panama, E. of Cocos Island and Cape St. Lucas—Panama Bay (Dall); (?) Amboina (Rumphius).

*Description.*—In general, the shell is not unlike that of *hians*. The ribs are " more numerous (45) and closely arranged," and the carinal knobs are more frequent and less prominent. The carina bears " interrupted undulations " (? continuation of the ribs, as in *A. nouryi*). On the whole the carina is narrower than that of *hians* and *nouryi*. The " submargin of sinus and spine [auricle] " are dark purple in colour. The whole surface except the umbo is minutely papillose. The aperture is markedly auriculate.

*Remarks.*—I am rather doubtful as to whether this form is not merely a subspecies of *hians*. Certainly the carinal knobs and the ribs are more numerous, but there is evidently a good deal of variation in *hians*. I have not seen any specimens exactly like *cornuta*, so I am unwilling to assert that it is referable to *hians*.

The figure 4 on Pl. XVIII of Rumphius' work may possibly be this form, and as this figure is cited by Solander for his *A. navicula*, the latter name may have priority over Conrad's, but from Rumphius' figure alone I would not care to decide.

Dall (*l.c.*, p. 226) regards Solander's *navicula* as a subspecies of *hians*. He does not seem to entertain the idea that Rumphius' figure may indicate the form described by Conrad as *cornuta*.

*Cornuta* has a good deal in common with *böttgeri* (see p. 195), but I think the following features serve to differentiate at least the type-specimens. *Cornuta* has a narrower keel than *böttgeri*; it is longer and not so deep, and there seem to be no auricles in *böttgeri*.

### **Argonauta nouryi**, Lorois.

(Pl. II, fig. 2, Pl. III, fig. 1.)

*Argonauta Nouryi*, Lorois (1852, Jan., p. 10, Pl. I, fig. 5).
,, *gruneri*, Dunker (1852, March, p. 48).
,, *Nouryi*, Conrad (1854, p. 333).
,, *Gruneri*, Dunker (1865, p. 29, Pl. IX, figs. 1, 2), Reeve (1861, Pl. 3, fig. 2*b*).
,, *Argo*, forma *mutica*, Martens (1867, p. 104).
(?) ,, *gruneri*, Sowerby (1864, p. 263, Pl. 258, fig. 9).
,, *Nouryi*, Tryon (1879, p. 138, Pl. 50, figs. 126, 127).
,, *nouryi*, Dall (1908, p. 224).

*Type*.—Not traced.

*Specimens seen*.—Three from the Marquesas (B.M.).

*Distribution*.—E. of the Marquesas (Lorois), Marquesas (Dunker; B.M.); "Pacific Ocean about the Equator" (Conrad); Gulfs of California and Panama, and off Acapulco (Dall); coast of Peru (Scammon, *fide* Dall).

*Description*.—The shell is of small size (type, 58 mm. long; Brit. Mus., 55 mm.; Dunker, 50 mm.). The whorls increase in size very rapidly and the last is very elongate. Viewed laterally it is much shallower than is usual in the genus. The edges of the aperture are almost straight, and none of the described and other examples known to me are auriculate. The sides, when viewed *en face*, are splayed outwards somewhat.

The surface is closely covered with low ribs, those most recently formed being somewhat undulating. Many of the ribs are forked (though none are so shown in the type and very few in Dunker's figure), and there are usually several secondary ribs. The keel is narrow and well-marked proximally, and is furnished with very dark and acute knobs. It becomes wider and less well-defined distally, the knobs more or less vanish, and the whole contour is rounded off and traversed by continuations of the ribs, which usually break up into large granules over the carinal area. In addition, the whole surface is covered with a fine granulation.

*Habits*.—From Conrad's account of the capture of some examples of this species in mid-Pacific, it seems to be gregarious or at least to live in temporary swarms.

*Remarks*.—This is a very distinctive form owing to its narrow elongate last whorl, and seems to vary very little except in the ribs (as noted above).

### **Argonauta nodosa**, Solander.

*Nautilus tenuis*, Rumphius (1705, p. 63, t. XVIII, figs. 1–3).
(?) Quallebootge, Vallentijn (1726, p. 519) (cited by Orbigny).
*Cymbium* . . . Gualtieri (1742, t. 12, fig. B).
*Nautilus tenuis* (pars), Hill (1752, p. 122).
,, *sulcatus*, Klein (1753, p. 3, No. 4).
"Reiszbrei-Nautilus," Knorr (1757, tom. VI, p. 62, t. XXXI).
*Nautilus tenuis*, Seba (1758, tom. III, p. 176, t. LXXXIV, fig. 4).
*Argonauta argo* (pars), Linné (1758, p. 7081).
Nautile . . . Meuschen (1767, p. 9, Nos. 52–58).
Nautile . . . Davila (1767, p. 109, Nos. 85, 86, 87 (?), 88).
"*Nautilus velificans*," etc., Martini (1769, tom. I, pp. 221, 229, t. XVII, fig. 156 (?)).

" Nautile . . . à stries tuberculeuses," Favart (1775, tom. II, pp. 425, 426).
" Nautile à grains de riz," Favanne (1780, tom. I, p. 714, Pl. VII, fig. A 9).
*Argonauta*, ( ?), Gronovius (1781, p. 281, No. 1216).
*Argonauta tuberculata*, Bolten (1798, p. 71).
" Knötig gestreifte Papier-Nautilus," Schroeter (1782, p. 51, No. 274, t. XL, fig. 274).
*Argonauta nodosa*, ( ?) *bibula*, Solander (1786, p. 96).
" *Papier* Nautilus, b " Kaemmerer (1786, p. 29).
( ?) *Argonauta oryzata*, Meuschen (1787, p. 252, No. 133 (not seen).
*Argonauta argo* (pars), Gmelin (1790, p. 3368).
,, *tuberculatus*, Shaw (1791, XXIII, tab. 995).
,, ,, var. b, Bruguière (1792, tom. I, p. 123).
,, *nodosa*, Humphrey (1797, p. 6, No. 81).
" Argonaute à grains de riz," etc., Montfort (1802, tom. III, p. 307, etc.).
*Argonauta argo*, var. 4, Turton (1802, IV, p. 304).
,, *vitrea*, Perry (1811, Pl. XLII, fig. 1).
,, ,, Dillwyn (1817, p. 334).
,, *tuberculosa*, Schumacher (1817, p. 260).
" Argonaute à grains de riz," Blainville (1818, p. 445, Pl. " Juin," fig. 1, A, B, C) (*fide* Orbigny).
*Argonauta tuberculata*, Wood (1818, p. 62, No. 2).
,, *tuberculosa*, Lamarck (1822, p. 652).
,, Bowdich (1822, Pl. XIII, fig. 4).
,, *tuberculata*, Férussac (1822, p. 552, No. 3).
,, ,, Mawe (1823, p. 80, t. 18, fig. 2).
,, *tuberculosa*, Blainville (1826, p. 212, Pl., fig. 1*a*, *b*).
,, *tuberculata*, Orbigny (1826, p. 138).
,, ,, Eichwald (1830, p. 34).
,, ,, Orbigny (1840, p. 169, Pls. 3 & 4).
,, *nodosa*, Gray (1849, p. 32).
,, *tuberculosa*, Sowerby (1864, p. 264, Pl. 257, fig. 3).
,, *tuberculata*, Martens (1867, p. 104).
,, *tuberculosa*, Küster (1868, p. 5, Pl. I, fig. 4).
,, *nodosa*, Tryon (1879, p. 140, Pl. 50).
,, *gracilis* and *tuberculata*, Kirk (1885, p. 58, Pl. XIII).
,, *nodosa*, Dall (1908, pp. 226, 228).
,, *nodosa*, Verco & Cotton (1928, p. 128).

(Dall (*l.c.*) cites *A. bibula*, Bolten (*l.c.*, p. 71), which was based on Martini (1769, Pl. 18, fig. 160). The latter is a poor figure, and it does not seem to represent a tuberculate form. Orbigny (1840) cites " Orbigny, Prodr. p. 48, No. 3 " (where ?).)

*Type.*—Not traced.

*Specimens seen.*—(*a*) In Brit. Mus.

One from Tasmania (M.C.); six from New Zealand (Sinclair, M.C.; 42.5.17.2; 1913, 7.8.1. and ?); one from N. Australia (57.11.18.79); five from Brazil (Cuming, and ?); eight from unknown localities (Coll. Cracherode and Broderip, etc.).

(*b*) In M.H.N., Paris.

One from ? locality ( ? type of Lamarck's *tuberculosa*) ; specimens from Brazil, Moluccas, " Nouvelle Hollande," " Asie."

*Distribution.*—" Les Grandes Indes," Mozambique, Cape of Good Hope (Orbigny (1826)); New Zealand (Brit. Mus.; Kirk); Moluccas (Rumphius); N. Australia (Brit. Mus.); S. Australia (Verco & Cotton); Tasmania (Brit. Mus.); New Jersey ( ?) (Tryon); Cape of Good Hope (Tryon); Chiloe (Gray); Brazil (Brit. Mus., etc.); Phillipine Is. (Hidalgo).

*Description.*—The shell attains a large size. The largest I have seen is 215 mm. in diameter. The keel is rather narrow, being 15–11% of the diameter. The carinal knobs are usually very prominent and close set, but in some adult specimens they are very low (see below). Auriculate forms occur in both young and old specimens, though the higher frequency of eared forms is in the young. The eared forms are moderately wide, the interauricular width being about 42% of the main diameter. The surface is covered with numerous fairly prominent ribs, which, towards the keel, are broken up into a series of isolated tubercles. The tuberculation is often very regular, the tubercles of one rib corresponding to those of its neighbour. The number of ribs is uncertain owing to a good deal of branching, but in a specimen 182 mm. in diameter there are visible 20 complete ribs stretching out from the callus. The knobs of the keel are numerous, and in a large specimen (182 mm.) 37–38 are visible in lateral view. The earlier knobs are sometimes (but not always) brown.

I have not seen the animal itself. Orbigny (*l.c.*) gives a short account of a female having a total length of 216 mm., of which the arms are 62%. The latter are in the order 2.1.4.3. The body is very slender (width-index 53%), the head narrower than the body with very prominent eyes. The colour was " partout blanchâtre, tacheté de brun-rougeâtre . . ." Orbigny comments on certain differences between the mandible of this form and that of *A. argo*.

*Remarks.*—Though the shell of this species is clearly distinguished from its fellows by the rough tuberculation, there are evidently two well-marked varieties—one with very large carinal knobs and coarse sculpture, the other with low knobs and fine sculpture. I am somewhat uncertain as to the distribution given above, as some of the early records are questionable.

### Species of Uncertain Status.

1. *Argonauta rufa*, Owen (1838, p. 114 (name only)), Gray (1849, p. 34). Gray only alludes to this as " animal and shell thick, red " (!). The type cannot be traced.

*A. conradi*, Parkinson (1856, p. 386), from " New Nantucket," Pacific Ocean. Dall thinks this may be a form of *dispar* (= *cornuta*).

*A. fragilis*, Parkinson (*l.c.*, p. 387). Possibly based on an abnormal specimen, as Dall thinks.

*A. pacifica*, Dall (1869, p. 238), *id.* (1871, p. 95). The status of this is very uncertain.

*A. geniculata*, Gould (1852, p. 470), *id.* (*Otia conchologica*, p. 231). The shell is not figured.

*A. striata*, Perry (1811, Pl. XLII, fig. 3), may be a small example of *argo*.

A good many unnamed specimens of *Argonauta* have been recorded, but I have not included these in the list. Perry's *A. rotunda* (*l.c.*, fig. 2) is a *Carinaria*, Turton's *A. arctica* and *cornu* (1802, p. 305) probably Pteropods.

Diagnosis of Species of *Argonauta*.

The following summary method of diagnosis of the six species recognized in this work may be employed. It must be remembered that in several characters there is much overlapping among the species.

*A.* 1. *A. argo.* Shell compressed and keel very narrow. Ribs close, numerous and bifurcating.

*B.* 2. *A. hians.* The keel broad. Ribs about 32 in number. Carinal knobs very prominent, about 15–23 in number.

3. *A. cornuta.* The keel broader than in 1, but narrower than that of 2 and 4. Ribs about 45. Knobs about 30.

4. *A. böttgeri.* Keel very wide. Ribs 30–45. Knobs (?) 14–33. ? Inauriculate.

*C.* 5. *A. nouryi.* Characterized by the long and shallow body whorl.

*D.* 6. *A. nodosa.* The ribs are regularly broken up into mainly coarse tubercles.

## Family 2. Ocythoidae, Gray.

The web is almost entirely absent. The adhesive-organ is highly complex. Both water vascular canals are present in the female and have been recorded as functioning as oviducts. Ventral water-pores are present. The radula is heterodont and not unlike that of certain Teuthoidea. The gills have 24 filaments in each demibranch. There is no secondary "shell" and no shell-vestige.

### Genus, **Ocythoë,** Rafinesque, 1814.

With the characters of the family.

*Type of the genus.—O. tuberculata*, Rafinesque.

### **Ocythoë tuberculata,** Rafinesque.

(Text-fig. 27.)

*Ocythoë tuberculata*, Rafinesque (1814, p. 29).
*Octopus tuberculatus*, Risso (1826, p. 3).
,, ,, and "P. di Ferrussac" delle Chiaje (1830, pp. 41(?), 56).
(?),, *veranyi*, Wagner (1829, p. 338).
,, *pictus*, Blainville (1828, p. 8).
*Philonexis tuberculatus*, D'Orbigny (1840, p. 87, Pl. 23).
*O[ctopus] catenulatus, id.* (t. c., Pl. 6, *bis* and 6 *ter*, 23).
*Octopus tuberculatus*, Cantraine (1841, p. 19).
,, ,, Delle Chiaje (1841, p. 3, Pl. 3 ; 1841*a*, p. 65).
,, *catenulatus*, Philippi (1844, p. 201).
*Philonexis tuberculatus*, Gray (1849, p. 26).
*Octopus catenulatus*, Vérany (1851, p. 37, t. 13 (♀)).
,, *carena*, Vérany (t. c., p. 34, t. 14, figs. 2, 3 (♂)).
*Hectocotylus octopodis*, Vérany (t. c., t. 41).
*Tremoctopus carena*, Vérany and Vogt (1852, p. 157), *id.* (*l.c.*).
*Philonexis tuberculatus*, D'Orbigny (1855, p. 206).

*Octopus carenae* and *Philonexis tuberculatus*, Adams (1853, pp. 19, 22).
„ *tuberculatus*, Risso (1854, p. 71).
(?) *Parasira catenulata*, Steenstrup (1860, p. 333).
„ „ Keferstein (1865, p. 1449).
*Philonexis* „ and (?) *carena* Targioni Tozzetti (1869, pp. 589–90).
*Parasira catenulata* and *tuberculata*, *id.* (1869*a*, p. 149).
*Octopus granulatus*, Verrill (1878, p. 210 in error, cf. *id.*, 1880*a*).
*Parasira catenulata*, Tryon (1879, p. 132).
„ *carenae*, *id.* (*l.c.*).
*Ocythoë tuberculata*, *id.* (*l.c.*).
„ „ Steenstrup (1880, p. 104).
*Philonexis reticularis*, Tiberi (1880, p. 13).
„ *tuberculatus*, *id.* (*l.c.*).
*Parasira catenulata*, Verrill (1880*a*, p. 293).
*Tremoctopus catenulatus*, Brock (1880, *passim*, t. XII, fig. 10 F).
„ *carenae*, *id.* (*l.c.*).
*Parasira catenulata*, Brock (1882, pp. 570, 588).
„ „ Verrill (1882, p. 362, Pl. XXXIII).
*Philonexis tuberculata*, Ninni (1884, 161).
*Ocythoë* „ Hoyle, (1886, p. 5).
*Parasira* „ Fischer (1887, p. 335).
*Ocythoë* „ Steenstrup (1887, p. 61).
*Tremoctopus döderleini*, Ortmann (1888, p. 642, t. 20).
*Ocythoë tuberculata*, Colombatovič (1890, p. 5).
„ „ Carus (1890, p. 457).
„ „ Jatta (1896, p. 198, Pls. 6, 7 and 19).
„ „ Joubin (1900, p. 26).
„ „ Hamlyn-Harris (1903, p. 350).
„ „ Marchand (1907, p. 368, figs. 47–53).
„ „ Lo Bianco (1909, p. 653).
„ „ Wülker (1910, p. 4).
„ „ Berry (1912, p. 385).
„ „ Naef (1912, p. 198).
„ „ *id.* (1916, p. 17).
„ „ Berry (1916, p. 3).
„ „ *id.* (1920*a*, p. 155).
„ „ Naef (1922, p. 291).
„ „ *id.* (1923, p. 749).
„ „ Degner (1925, p. 81).
„ „ Naef (1928, p. 295).
„ „ Sasaki (1929, p. 26, Pls. III, VIII, text-fig. 8).
„ „ Joubin (1929*a*, p. 9, figs. 12–13).

*Type.*—Not traced (originally in Coll. Orbigny, *fide* Isnard (1922, p. 31)).

*Specimens seen.*—(*a*) In British Museum.

One (♂) from Messina (Rüppell); one (♂) from Naples (Norman); five (♂) from unknown localities; one (♂) from "the Atlantic"; one (♀) from Naples (98.5.21.360); one (♀) from Nice; one (♀) from Egypt; one (♀) from Madeira; two (♀) from unknown locality (79.1.20.4–5).

(*b*) In M.H.N., Paris.

Eight (♂) from Nice, one (♂) from " Mediterranean "; three (♂) from unknown locality; one (♀) from " Pacific "; one (♀) from Nice.

(*c*) In Mus. Oceanogr., Monaco.

One (♂) from (?) N.E. Atlantic (" Pr. Alice," Stn. 656); one (♂) from Nice; two (♂) from Monaco; one (♂) from Stn. 1874 (" Pr. Alice "); three (♀) from Monaco.

*Distribution.*—Mediterranean (*passim* (Auctt.)); Madeira (B.M.); N.E. Atlantic (Monaco); " W. Indies " (Verrill); Vineyard Sound, Massachusetts, (?) in shallow water (Verrill); Japan (Misaki, Wülker, Sasaki); Tokio (Ortmann); Santa Catalina Id., California (Berry); " Pacific Ocean " (M.H.N., Paris). Not recorded in Red Sea (Wülker), Indian Ocean (Massy), South Africa (Robson, Massy).

*Description.*—(a) *The female.*—The body is large, as compared with the head and arms. It is ovoid with a more or less rounded apical region. The maximum diameter is at one-third " of the way back " (Sasaki), or about five-twelfths (Naef (fig. 450), Brit. Mus.) of the distance from the ventral mantle-edge to the apex. The maximum width is 77–64% of the length. The head is small and distinctly narrower than the body. Its maximum width is 57–42% of the length. The eyes are of moderate size. The arms are 70–61% of the total length, there being no significant difference between Mediterranean and Eastern forms in this respect. The formula varies very much. More often 4 is the longest and 1 the next (that order being sometimes reversed) with $2>3$ or $2=3$. The suckers are small. They are cylindrical and prominent and arranged in two widely alternating series. The adoral ones are the largest, and the rest slowly decrease outwards. They are situated on the edge of the arms and are connected by a low, thin membrane (p. 38). The sucker is truly Octopodine and consists of suctorial and basal chambers. The dorsal arms are provided with a distinct dorsal membrane, which attains its maximum depth (about twice as deep as the arm's thickness) at a little more than one-third of the length. This is absent or only very slightly indicated on 2 and 3, but is found on 4. There is no web between any of the arms. The colour is described in detail by Jatta (*l.c.*) and Naef (1923). The general tint in life is a light blue modified by other tints through the contractions of the chromatophores. The sides and ventral surface are covered with hard pointed tubercles set 4–5 mm. apart, and connected one with another by a characteristic network of low cuticular ridges.

The mantle-aperture is very wide and extends dorsally above the eyes.

The funnel is long and projects well beyond the mouth. It is tubular with a large circular aperture and the distal third or half of its length is free. There is a \/\/ -shaped funnel-organ. The locking-apparatus is highly characteristic. The cephalic element consists of a prominent stud with outward flanged head and a deep but weakly-defined negative portion. The latter receives the prominent positive pallial element, while the positive cephalic element fits tightly into a deep cavity on the pallial side. There are two water-pores on each side of the funnel at the base of the fourth arms.

*The alimentary system.*—The jaws are normal, except that (*fide* Naef,

*l.c.*, Pl. 18, fig. 11) the rostral lamella of the lower mandible is deeper and longer than the gular lamella. The radula (Text-figs. 3–4) has been discussed on p. 11 and seems to be somewhat variable. The median has a long mesocone and small ectocones. The first lateral has a very large entocone and small ectocones. The second lateral has a narrow base, a long, slender mesocone and a fairly prominent entocone. The third lateral is narrow, with a fairly large base. There is a diminutive marginal.

*The gills* have about 18–24 filaments in each demibranch. The inner demibranch is rather shorter than the outer. As compared with the gill of *Octopus* that of *Ocythoë* shows certain peculiarities, viz. (1) The branchial canal is very small (? Decapod character), and (2) there is a marked amount of asymmetry.

The central nervous system has been described by Pfefferkorn (1915).

Fig. 27.—*Ocythoë tuberculata* (♀). Adhesive-apparatus. × 1.

The reproductive organs have been figured and described by Brock (1882, Pl. XXXV, fig. 12) and by Sasaki (*l.c.*, text-fig. 8). The Japanese and European forms agree in having a very short proximal oviduct and an excessively long distal oviduct terminating in an expanded vaginal portion. Sasaki shows the oviduct as very thick and almost as wide as the subcircular oviducal glands. Brock shows it as slender and the glands elongate and ovate. I think, however, that this difference may be due to the fact that Sasaki's specimen was in an active reproductive phase. Both water-canals are present and normal ( ?). Sasaki states (*l.c.*, p. 25) that the water-canals are used as oviducts and that the eggs " attain development " in the renal sacs. According to Brock the animal is viviparous.

I have been unable to find any certain trace of a shell-vestige in this form.

The female of this species attains a very considerable size. Naef (*l.c.*, p. 756) says it is sometimes over 30 cm. (1 foot) without the arms.

I have seen one in the Institut Océanographique, Monaco, which was 280 mm. from the apex of the body to the eye.

(b) *The male.*—The sexually mature male has an ovoid mantle and a relatively larger head than the female. The funnel projects to about the same extent. There are no ventral cuticular warts. The second arms are only about half the length of the first. I have had no undamaged male specimens to measure, and must rely on other statements. Jatta (*l.c.*, p. 202) gives the size as 80, 50, 50, 80 mm. Naef (*l.c.*, fig. 453) figures a specimen from which I estimate the length of the arms as follows: 95, 48, 36, 95 (all $\pm 5$). The arms in this specimen are about 76% of the total length and are thus distinctly longer than in the female, and it will be seen that there is a very marked disparity in size between 1 and 4 as against 2 and 3. Another difference between the male and female is the absence in the former of both the dorsal arm-keels and lateral arm-membranes.

*The hectocotylus.*—The fully-extended and cast-off organ consists of a proximal sucker-bearing part. This has a somewhat expanded oral surface bearing two rows of small globular suckers with very small apertures connected by a membrane as in the female arms. Beyond this is the Penis-sac, an oval structure which contains the coiled-up penis. The point of exit of the penis lies just proximally of the end of the sucker-bearing part.

There are no very recent figures as to the size of the hectocotylus in this species. In the Musée d'Histoire Naturelle, Paris, there is a specimen from Nice with the sucker-bearing part 130 mm. long and the penis 270 mm.

The spermatophores, which have been figured and described by Vérany and Vogt (*l.c.*), are remarkable on account of the enormous size of the reservoir and the shortness of the rest of the structure.

The internal reproductive organs have been described and figured by Marchand (*l.c.*) and appear to be peculiar in certain respects. The left water-canal only is present.

The proximal vas deferens (Marchand, fig. 50) has an ampulla at its proximal end. The series of spermatic glands are remarkably elongate, and the three glands are but little distinguished one from another. The prostate (accessory gland) has a long and slender duct. The appendix of the prostate ("Blindsack") is very small and rudimentary. Needham's organ is rather peculiar in that it is glandular in its entire extent and ends in a long, narrow tubular portion. Marchand says (p. 375) that it has entirely lost the function of a spermatophore-reservoir. If I understand Marchand correctly (*l.c.*), this function is taken over by a large penial diverticle and "das vas efferens von *Ocythoë* entspricht dem unteren Abschnitt des Penis der übrigen Octopoden."

*Remarks.*—Although this species has been recorded from areas widely separated as the Mediterranean, Japan and the coast of California, the available descriptions are not sufficient to enable us to say if the determinations are correct or if there is more than one subspecies in this very wide area. The specimens described by Sasaki and Berry seem to belong to the same species as that found in the Mediterranean.

The earlier writers were in some confusion as to the right use of the name *Ocythoë*. For Steenstrup's *Parasira catenulata* see p. 215.

Family 3. Tremoctopodidae, Tryon (emend.).

Pelagic Argonautida with a simple and Octopus-like adhesive-apparatus and dorsal and ventral water-pores. The first arms are much longer than the other pairs, and are joined together and to the second arms by a characteristic web, the third and fourth arms having scarcely any web at all. The shell-vestige is present. Sexual dimorphism is less marked than in *Argonauta*. The radula resembles that of the Heteroglossa. The funnel-organ is formed by a number of ridges. There is no secondary shell.

Genus **Tremoctopus,** delle Chiaje 1830 (?).

With the characters of the family.

*Type of the genus.—T. violaceus,* delle Chiaje.

*Remarks.*—A good many species of *Tremoctopus* have been described. In 1923 (*l.c.*, p. 734) Naef (following Jatta) expressed the opinion that all these species are really forms of *Tremoctopus violaceus*, though there are distinct local forms. In the older descriptions there is a lack of comparable data, and the descriptions are often defective; so that any determination of the identity of the described species is not really possible. The interesting metamorphic changes and the differences between the male and female (not realized by early workers) constitute further difficulties in the way of a clear understanding of the identity and relationships of the forms previously described. This same position was arrived at by Berry (1914, p. 285), though he thought it might be possible to recognize a Pacific species, *T. gracilis* (Eydoux & Souleyet). Joubin (1929*a*, p. 2), however, thought there are at least two distinct species of *Tremoctopus* (to judge from the male), and he treated Berry's Hawaiian "*violaceus*" as the same as *T. quoyanus* (Orb.). I have retained as distinct species *T. violaceus, microstoma, gracilis, dubius, ocellatus, hirondellei* and *T. scalenus*, though all but the first-named seem to me to be of doubtful position. All the other forms I have no option but to treat as forms of *T. violaceus*. I agree with Joubin that marked differences occur, *e.g.*, between the hectocotylus of Berry's "*violaceus*" and the Atlantic specimen figured by himself. But the same is true of all the Atlantic and Mediterranean specimens of which the hectocotylus has been figured (see below). It might be claimed that the *violaceus* of Jatta, Naef and Joubin are all specifically distinct, but actually their other characters are too much alike for this. The status and characteristics of the various forms now included in the synonymy of *T. violaceus* are discussed on p. 212.

**Tremoctopus violaceus,** delle Chiaje.

(Text-figs. 28, 29.)

? *Octopus vérany* [i], Wagner (1829, p. 388).
*Tremoctopus violaceus*, delle Chiaje (1830 (?), taf. 70, 71).
*Octopus velifer*, D'Orbigny (1830 [=1840, Pls. *fide* Jatta], Pls. 18, 19).
,, (*Philonexus* [sic]) *quoyanus, id.* (1835, p. 17, Pl. 2).
,, (*Philonexis*) *atlanticus, id.* (p. 19, Pl. 2).
,, ,, *semipalmatus*, Owen (1838, [p. 111] Pl. 21).

*Octopus velatus*, Rang (1837, p. 60).
,, *hyalinus*, *id.* (*l.c.*, p. 66, Pl. 92).
*Philonexis velifer*, Orbigny (1840, p. 91, Pls. 18, 19, 20, 23).
,, *quoyanus*, *id.* (p. 96, Pls. 16, 23).
,, *atlanticus*, *id.* (p. 98, Pl. 5).
,, *microstomus*, *id.* (p. 100, Pl. 10).
*Tremoctopus violaceus*, delle Chiaje (1841, p. 6; 1841*a*, p. 66, pl. 4, etc.).
,, ,, Kölliker (1844, p. 161).
*Octopus velifer*, Philippi (1844, p. 201).
*Philonexis velifer*, Orbigny (1845, p. 205).
,, *quoyanus*, *id.* (*l.c.*, p. 202).
,, *microstomus*, *id.* (*l.c.*, p. 204).
,, *atlanticus*, *id.* (*l.c.*, p. 203).
,, *hyalinus*, *id.* (*l.c.*, p. 205).
*Octopus köllikeri*, Vérany (1847, p. 513).
*Tremoctopus violaceus*, *quoyanus*, Grey (1849, p. 27).
,, ,, Kölliker (1849, p. 67).
*Octopus koellikeri*, Verany (1851, p. 33, taf. 11).
,, (*Tremoctopus*) *violaceus*, *id.* (*l.c.*, p. 41, taf. 14–16).
,, *gracilis*, *dubius*, Eydoux & Souleyet (1852, pp. 13, 15, t. I).
*Philonexis microstomus* (= *koellikeri*), *T. violaceus*, Troschel (1857, pp. 44, 50).
*Tremoctopus violaceus*, Keferstein (1866, p. 1449).
,, ,, Targioni Tozzetti (1869, p. 591).
,, *velifer*, *quoyanus*, Woodward (1875, p. 165).
,, *violaceus*, *microstomus* (?), *gracilis* (?), *dubius* (?), Tryon (1879, pp. 130–131, t. 43).
,, *violaceus*, Tiberi (1880, p. 14).
,, ,, Brock (1880, *passim*, t. XII, fig. 10E).
,, ,, Brock (1882, p. 583).
,, ,, Ninni (1884, p. 159).
,, *quoyanus*, *atlanticus*, *gracilis* (?), Hoyle (1886, pp. 70–71).
,, *violaceus*, Fischer (1887, p. 335).
,, *quoyanus* (= *koellikeri*), Jatta (1889, p. 63).
,, *violaceus*, Colombatovič (1890, p. 7).
,, ,, (*microstomus*, *koellikeri*), Carus (1890, p. 457).
,, *microstoma*, Joubin (1893, p. 218, figs. 3–9).
,, ,, Jatta (1896, p. 204, tab. 6, 20).
,, (?) *quoyanus*, Hoyle (1904, p. 12, fig. A).
,, *joubini* (Hoyle, 1909, p. 258).
,, *violaceus*, Lo Bianco (1909, p. 656).
,, ,, Wülker (1910, p. 5).
,, ,, Naef (1912, p. 199).
,, *quoyanus* (?), Hoyle (1912, p. 276).
,, ,, Berry (1914, p. 281, figs. 8–10).
,, *atlanticus* and sp. (?), Chun (1914, p. 18).
,, *hyalinus* (?), Chun (1915, p. 478, Pl. 77).
,, *violaceus*, Naef (1916, p. 17).
,, ,, Massy (1916, p. 144, figs. 3–4).
,, ,, Wülker (1920, pp. 51, 56).

(?) *Tremoctopus hyalinus* (Thiele, 1920, p. 434).
*Tremoctopus violaceus*, (?) Joubin (1920, p. 30 (very young)).
,, ,, Naef (1921, p. 538).
,, ,, *id.* (1923, p. 735 and *passim*, figs.).
,, ,, (?) Degner (1925, p. 80 (young)).
,, (?) sp., Aguilar-Amat (1926, p. 139).
,, *violaceus*, Neviani (1927, p. 200, figs.).
,, ,, Sasaki (1929, p. 29, Pl. VIII, text-figs. 9, 10).
,, ,, Naef (1928, p. 299).
,, ,, Joubin (1929*a*, p. 1, text-figs. 1–11).

*Type.*—Not traced.

*Specimens seen.*—(*a*) In British Museum.

One from Messina; two from Nice (89.2.11.6, 98.5.21.363); one from 11° N., 26° W. (74.11.14.2); four from N. Atlantic (" Challenger "); three from " the Atlantic " (90.5.12.1–3); two from Muscat (97.1.13.4–5); two from Hawkes Bay, N. Zealand (1906.2.7.18); one from the S. Pacific (" Challenger "); one from New Guinea, Japan (" Challenger ").

(*b*) In M.H.N., Paris. Two from Nice; one from " Mediterranean."

(*c*) In Mus. Oc., Monaco. One from the Atlantic (" Princesse Alice," Stn. 1768).

*Distribution.*—Mediterranean (Auctt.); N. Atlantic (Joubin, Hoyle, etc.); Tropical Atlantic (Orbigny); S. Atlantic ? (Gray); Red Sea (Wülker); Sagami Sea (Wülker); Misaki, etc. (Japan) (Sasaki); New Zealand (Massy); Hawaii (Berry); 18° N., 134° W. (Hoyle); Valparaiso-Callao (Jatta); Sandwich Is., Tahiti W. Pacific (?) (Hoyle); New Guinea, Japan (as *gracilis*) (*id.*).

*Description.*—(a) *The female.*—In early life the head is large (usually wider than the body) and the eyes prominent (" *köllikeri* stage " (Naef)). In the adult the head is smaller but wider than the body. The latter is usually elongate-ovoid, but in quite large specimens (cf. Sasaki's Table (*l.c.*, p. 31) the body may be as wide as it is long. The arms in the young are in the order 1.2.4.3. The first arm is considerably (one-third or more) longer than the second. The fourth arm is about a third the length of the first and the third is still shorter. The adult is characterized by the loss of the extremities of the two dorsal arms. This very interesting and remarkable phenomenon is of regular occurrence, and the lost portions are usually (but not always) equal in length. The nature of the loss has been discussed by Naef (1923, p. 741). The suckers are in two alternating rows except towards the extremity of the first arms, where they are uniserial even in the adult (Sasaki, Naef, *l.c.*, fig. 442, but cf. text). They are imbedded in solid supports and seem to be connected on one side by the characteristic membrane (*v.* p. 38). In section the suckers are seen to be very weak and to consist of but a single chamber. The suckers are smallest on the first and second pair of arms and largest on the fourth.

The web undergoes a characteristic metamorphosis. In the *köllikeri*-stage it is not developed. In specimens about 6 mm. long in mantle-length (Berry) it shows some differentiation, A being deeper than E. In specimens 15 mm. long (Naef, *l.c.*, text-fig. 440) it shows the definitive condition, being deep in A and B and very shallow in C, D and E, and in addition it is continued up both sides of the first and the dorsal side

of the second arms. In Naef's figures 441–443, B is shown as slightly deeper than A. In the British Museum specimen and in Sasaki's examples it is much deeper. There is a very curious difference between Sasaki's specimens and those of Jatta, Naef and our Mediterranean examples in that the web in sector E is far deeper in the Japanese specimens ($\frac{1}{2}$–$\frac{1}{5}$ of sector B) than in the Mediterranean specimens (*c.* $\frac{1}{7}$).

There are two pairs of water-pores, one at the base of the dorsal arms and the other at the base of the ventral arms. Naef (*l.c.*) does not figure these in his *köllikeri*-stage, but they are well developed by the time the mantle is 15 mm. long.

The skin is more or less smooth. Actually it is covered with fine papillae, which in preserved specimens are barely perceptible. These have been studied by Tippmar (1913, pp. 538–539), who states that he could find nothing similar in the other Octopoda examined, and that they are very like similar cutaneous papillae in *Mastigoteuthis cordiformis*.

The colour of the living adult has been figured by Jatta (*l.c.*, Pl. 6, fig. 2). He describes it as "nella parte dorsale l'azzurro con una vaga sfumatura di color rosso carminio, nella parte ventrale il grigio perlaceo

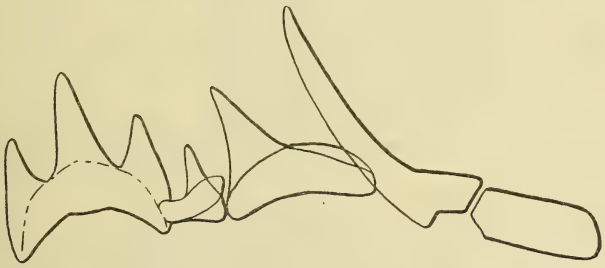


Fig. 28.—*Tremoctopus violaceus* ("Terra Nova"). Radula.

con sfumature gialliastre ed iridescenza argentina. Gli occhi sono azzurri." Jatta (*l.c.*, Pl. 7, fig. 23) shows a *köllikeri*-stage which seems to be covered with moderately-sized dark chromatophores. Joubin's "*microstoma*" (1893) has a very striking pattern of large chromatophores which does not agree with Reynaud's original figure, in which the latter are small and probably like those of Jatta. Berry's series of young (*l.c.*, p. 284) seem to have a characteristic pattern. It is not, however, possible to make taxonomic use of the pattern, as in the other forms the pattern has not been very well described. It seems, however, to be very distinct, *e.g.*, from that seen in Joubin's "*microstoma*."

The funnel is inconspicuous and of moderate size. It projects somewhat beyond the eyes. The funnel-organ consists of a number of rather irregular stripes, though in an early "*ocellatus*" stage these are preceded by a W-shaped organ. Jatta shows about 12, but Sasaki (*l.c.*, p. 30) says that there are as many as 100. It is a curious fact that the W-shaped foundation is not shown in the adult by Jatta, but it is plainly seen in Sasaki's figure of the adult. As Naef (*l.c.*, p. 743) said, this form of adult organ is unique in the living Dibranchiata.

The adhesive apparatus is like that found in most Heteroglossa, and consists of a fairly deep and long pallial element and a weak broadly triangular or rounded (Sasaki) cephalic element.

The gills exhibit as many as 14 filaments in each demibranch.

*Internal organs.*—The radula, as figured by Jatta and Naef, is Octopus-like. There is a tricuspid median with low mesocone and a small single-cusped admedian. The second laterals have a straight base and low, stout, marginal cusp. The third laterals are fairly slender and have a small square base. The marginals are square (Naef). The radula of "*microstoma*" (Joubin, 1893, fig. 8) is rather different in some respects, and I would not regard it as conspecific, nor would I think that figured by Massy (1916, "*violaceus*") and reproduced (corrected) here (fig. 28) is conspecific. Both these radulae were, however, taken from immature animals. The reproductive organs have been figured and described by Brock (1882) and Sasaki (*l.c.*). These authors agree in figuring a relatively long and slender oviduct. Below that point the figures differ in several important features, which I hardly think are due to possible difference in sexual maturity. Brock figures a very large receptaculum followed by a smaller oviducal gland and finally an irregularly swollen uterus. Sasaki shows a spermoviducal gland in two main parts, the first smaller than the second, followed by a narrow duct that swells out distally into an enormous uterine expansion "within which numerous fertilized eggs may be fixed." Sasaki (*l.c.*, p. 29) states that the water vascular canal is rudimentary, but Brock figures a pair of long canals and describes them (*l.c.*, p. 585) as following the normal course, though the left is rather shorter than the right.

*The shell-vestige* is a pair of straight solid rods measuring *c.* 14 × 4 mm. They do not exhibit the bend (or kink) seen in the vestige of the Octopodidae.

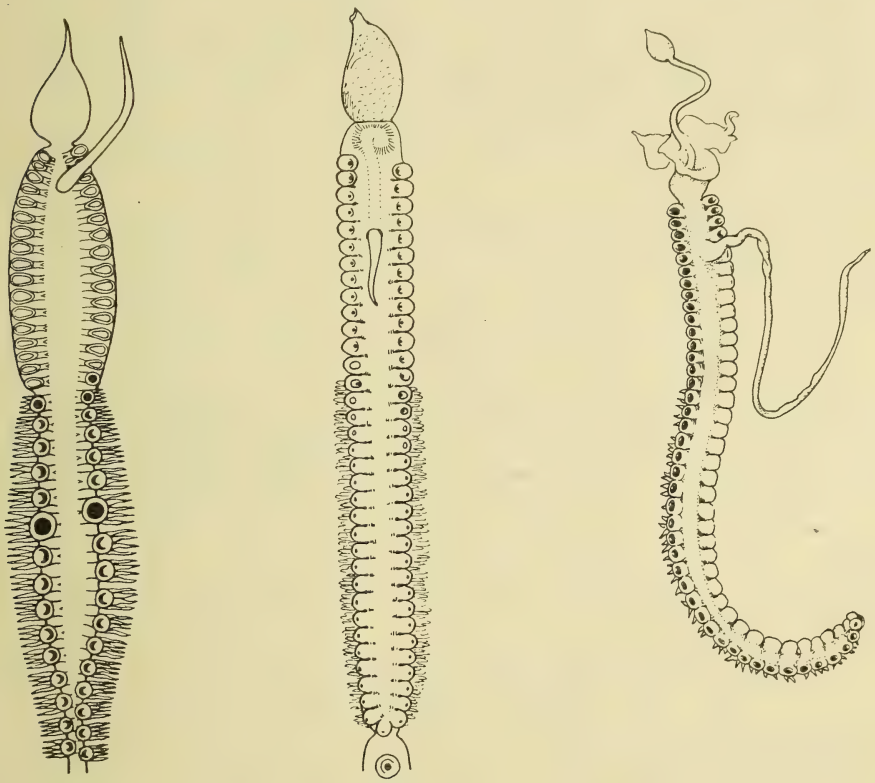
(b) *The male.*—Naef (*l.c.*, p. 744) points out that the *köllikeri*-stage of the male is in all respects identical with the female except in the character of the third arm. I have not had any very young males to examine and cannot criticize Naef's statement. From the available figures and measurements it seems to be true. Berry (*l.c.*, p. 284) does not differentiate the young males and females.

The adult male, according to Naef (*l.c.*, p. 747) undergoes the same modifications as the female, *i.e.* the dorsal web becomes large and the ventral remains small and the ventral suckers become larger than the dorsal. Berry and Naef agree in stating that the arms are shorter than in the females of equivalent size, and there is no trace of a differentiation of the dorsal arms.

*The hectocotylus.*—The modified portion of the third right arm in the adult male is divisible into three distinct areas—basal, median and distal. The basal and median portions exhibit a double series of closely-set rounded suckers with small orifices. Over the basal portion there is on each side, outside the suckers, a more or less regularly arranged double fringe of small processes. The median portion (beyond the fringed area) is devoid of these. Towards the end of this the "penis" projects from a small orifice on the oral surface of the arm. Beyond this the distal portion consists of the "penis-sac," an oval structure with an orifice at the apex. The development and fine structure of the various parts are described by Naef (*l.c.*, pp. 744–747).

The four most recent and best illustrated accounts of the hectocotylus in the adult (Jatta (*l.c.*), Naef (*l.c.*), Berry (*l.c.*), and Joubin (*l.c.*)) differ

in the details so much that I give them in tabular form below. As already suggested (p. 206) there are sundry well-marked divergences among the various examples assigned to this species, and those of the hectocotylus may be regarded as indicative of specific divergence. For the time being, however, I do not think it advisable to utilize them for such distinctions, as they are not accompanied by sufficiently clear divergences in other characters.



(*a*) (*b*) (*c*)

Fig. 29.—Hectocotylus of *Tremoctopus violaceus*.
(*a*) After Joubin, 1929*a*; (*b*) after Naef (1923); (*c*) after Jatta (1896).

| | Number of suckers (pairs) on fringed part. | Number of suckers (pairs) on median area. | Position of penis orifice. |
|---|---|---|---|
| 1. Joubin (1929*a*) | 16–15 | 17 (oblong : close) | apical (at the 3–4th sucker from the end) |
| 2. Naef (1923) | 20 (not 21 as in (*b*), fig. 29) | 13 (round : close) | subapical (at the 5th sucker) |
| 3. Jatta (1896) | 27–28 | 14 (between 1 & 2 : close) | subapical (at the 5th sucker) |
| 4. Berry (1914) | 27 | 19 (round : separate) | apical (at the 3rd sucker) |

In addition the arm figured in 2–4 has parallel sides, whereas in 1 the

basal and median areas are differentiated in outline. Finally, Joubin (*l.c.*, p. 6) seems to indicate a higher number of rows of fringes in his specimen, viz. five.

*Habits.*—Very little is known concerning this interesting form. It seems to be pelagic and (*fide* Vérany) gregarious. More than one author refers to its capture at night. Troschel, Joubin and Naef comment on the frequent occurrence of portions of Coelenterata ( ? tentacles of Medusae) on the arms of the young. Naef (*l.c.*, p. 737) actually found them in all the young specimens, and suggests that their presence may be adaptive, as the nematocysts may be a protection to the young Octopod. The oviposition and nidamentary rod discovered by Kölliker, which may represent the Argonaut shell, have been already alluded to (p. 25). Jatta says that the animal swims both by its funnel and by the arms and web.

*Remarks.*—The name of this form appeared first on Plate LXX of delle Chiaje's "Memoria." The volume of plates seems to have undergone an accident, as some copies (B.M., and (?) Oken's (*Isis*, 1836, p. 291)) did not have Plates LXX–CIX. At all events the missing plates were reproduced later in the "Descrizione" (1841). In 1836 Oken (?) (*l.c.*) describing the absent plates (? from a complete copy) gives the name as "70. *Tremoctopus* (*Loligo violaceus*). . . ." In the British Museum copy of the "Descrizione" it figures as "*Tremoctopus violaceus*."

The date is very uncertain. The incomplete volume of plates is dated 1822. Oken (*l.c.*) gives it as 1823–1829, Vérany as 1830 (1851, p. 44). It is possible that Wagner's *vérany*[*i*] and Orbigny's *velifer* may have a claim to priority. According to several authorities the latter is dated (name and figure only) 1830, but Mr. C. D. Sherborn (MS.) states that the date of the plate is uncertain. In this uncertainty it seems better to retain delle Chiaje's name. The exact character of *véranyi* is uncertain.

As already stated (p. 206), the forms placed in this species are not all alike and some of the differences seen are considerable. Owing to the reasons already given I do not consider it advisable to distinguish any as distinct species. I give, however, a brief summary of the various debatable forms. The position assigned to some of them is, in default of satisfactory evidence, quite arbitrary.

*T. quoyanus* (Orbigny) appears to be a typical (♀) juvenile form. Orbigny says the web is half as long as the arms (though it is not figured as such).

*T. atlanticus* (*id.*). I retain this in the synonymy of *T. violaceus* with some misgivings. It is very small (4 mm. mantle-length). The body is much wider than the head, an unusual feature in young *violaceus*, and the first arms show a precocious enlargement which are already over twice as long as the second and ten times longer than the third.

*T. microstoma* = *joubini* (Hoyle, 1909) (Joubin, 1893, *non* Reynaud). I think this is a juvenile form of *violaceus*. It is certainly far more like the young forms of that species than it is of Reynaud's species.

*T. hyalinus* (Rang, Orbigny). This species was figured by Orbigny before its description was published; but as it is doubtful whether

Orbigny's plates were published before his text, Rang's claim must be regarded as prior. The type was a very small animal (25 mm. over all). The shape of the head and the relative length of the arms are not like those of the young *violaceus* of more or less equivalent size figured by Naef (text-fig. 440). But it may for all that be referable to this species. "*T. hyalinus*, Rang" (Joubin, 1900, p. 27) is, I think, after examining the original specimen, an *Eledonella*.

*T. semipalmatus* (Owen), has the general appearance of a young *violaceus*, but (*a*) its very prominent and semipedunculate eyes and (*b*) the relative sizes of the arms do not agree with those of *violaceus* of equivalent size.

*T. köllikeri* (Vérany). I accept Naef's treatment of this form, which was apparently founded on large series of young specimens. Vérany's *köllikeri* seems to be a characteristic phase of juvenile *violaceus*, though it must be noted that it was rather larger than those figured by Naef.

*T. gracilis* (Hoyle, 1886, *non* Eydoux & Souleyet) is, I think, from an examination of the type, a young *violaceus*.

It is difficult to say if the Oriental and Japanese forms are really identical with the European. In the external characters I cannot distinguish any differences that one could rely upon. The differences in the female genitalia are quite marked (p. 210). The various notable differences in the hectocotylus have been already noticed (p. 211).

### Species of Uncertain Status.

Some of the forms described below are undoubtedly representatives of distinct species.

*Tremoctopus* (?) *hirondellei*, Joubin (1895, p. 10, Pl. I, figs. 1–2; Pl. II, figs. 1–3). 44° 28′ N., 46° 48′ W., surface.

This is represented by a very small specimen only 9 mm. in total length. The arms are very short (4 mm.) and practically of equal length. The web is very much developed and attains a maximum of 50% of the arms. The body is short and very broad and more or less like the typical *köllikeri*-stage of *T. violaceus*. The size and order of the arms, which according to Naef's figure (*l.c.*, p. 437) in smaller specimens show signs of differentiation, seem to distinguish this from *violaceus*.

It is distinguished, moreover, from *T. violaceus* by the adhesive-organ, which is far better developed than in that species. There is a large, rather oblong, negative cephalic element. It is very deep and well defined, and receives a prominent stud-like pallial element. It is plain that we are here dealing with a very different organ from that of *T. violaceus*, and it seems to me likely that Joubin's species may be a representative of a different genus (though not of *Argonauta*, cf. p. 183). However, as the adult is unknown, it is undesirable to proceed any further in this matter. The external part of the funnel is very weak and almost entirely subcutaneous, but the intra-pallial part is highly developed. Possibly some of the short-armed larval forms are related to, or even identical with, this form.

*Tremoctopus scalenus*, Hoyle (1904, p. 13, Pl. 4, figs. 6–9). Off Cape Mala, W. Panama, surface.

This is remarkable, owing to the excessive length of the second arms. The length (in mm.) of the arms is as follows :—R. 40, 100, 50, 25; L. 36, 90, 24, 26. The shape of the body is uncertain as the specimen was damaged, but it seems to have been very long and narrow (17 × 9). The head is very small, and the eyes very prominent and almost pedunculate. The suckers are widely spaced and alternating. The funnel is large and prominent, but does not pass the level of the eyes. " The aquiferous pores can no longer be made out." The web is either absent or very badly damaged. The specimen measures 120 mm. over all.

I find it very difficult to decide if this is really a Tremoctopus rather than a member of the Octopodidae.

*T. mycrostoma* [sic] (Reynaud (1831, p. 23, Pl.)) is very small (4 lines without the arms). The arms are in the order usually found in *violaceus*, but the head and eyes are very small and the body is exceptionally long for a young *violaceus*. It was taken in great quantities in 33° N. and 35° W. (of Paris).

*T. gracilis* (Eydoux & Souleyet, 1852, p. 13, Pl. I) has a mantle-length of 6 mm. The first and second arms are relatively much longer than in Naef's *koellikeri* figures (which are almost of the same size), and the web is already 25% of the arms, and E is very well developed. It may be a form of *violaceus*, but I am rather doubtful. Found in the Pacific Ocean, 8° N., 106° W.

*T. dubius* (*id.*, *l.c.*, p. 15, Pl. 1) is very minute (3 mm. in mantle-length). The arms, as in *hirondellei*, are not so long as the body. The identity is very doubtful. It was taken off the island of Bourbon.

" *T. hyalinus*," Chun (1915, p. 478, Pl. LXXVII, figs. 1, 4–6), taken at " Valdivia " Stn. 49 (off Cape Palmas, W. Africa). Chun was evidently guided by the fact that in his specimen the eyes are very prominent and sub-pedunculate (?) as in *hyalinus*, but the disparity between the arms is far more marked than in Rang's species.

*T. ocellatus*, Brock (1882, p. 601, Pl. XXXVII, figs. 1, 2). Messina. The natural size figure shows a specimen with a mantle-length of 35 mm. and arms in the order 1, 2, 4, 3. The dorsal arms have a rather small apical portion removed. The web is very low and the brachial membranes on the first arms are very long. In these respects the species is very unlike *T. violaceus*.

Brock considered that this form differs from *violaceus* in the great length of its dorsal arms and *velum* (by which he must mean the brachial membrane), and in the possession of two dorsal cephalic ocelli situated between the eyes. The brachial membranes are very much contracted in places and form " beutelförmigen Aussackungen," which Naef (*l.c.*, p. 740) thinks may serve to catch prey. At present all we can say is that the arms and the accompanying membranes are much longer than usual, and the web is shallower than in *violaceus*. I am doubtful whether the colour-differences are important.

## Family 4. Alloposidae, Verrill.

The body is gelatinous. There is no shell-vestige, and no secondary shell. Sexual dimorphism (?) moderate. The hectocotylus is provided with two lateral fringes of lobate processes, a free penis and a separate sperm reservoir. There are no water-pores. The radula tends to be like that of *Octopus*, but the admedian is larger and in one species is "Egopsid." An adhesive-apparatus may be present (?). The animal is probably planktonic and attains a very large size.

### **Alloposus,** Verrill, 1880.

With the characters of the family.

*Type of the genus.*—*A. mollis*, Verrill.

*Remarks.*—Steenstrup's "*Haliphron*" * (1859 and 1860), which was represented only by part of a hectocotylised arm, may be referable to this form, and, in that case, should have priority. According to Hoyle (1886, p. 73), there seems very little hope of ever establishing its true character. It seems to have shown no trace of the lateral fringes.

The "lateral commissures" uniting the head and mantle, on which Verrill laid so much stress, are not found in *A. hardyi* or *A. pacificus* (Sasaki, 1929) (but cf. p. 219). Sasaki neither records nor figures the adhesive system alluded to by Ijima, nor could I find one in *A. hardyi*. As pointed out later (p. 216), Verrill is not likely to have mistaken an adhesive system, had it occurred in *mollis*, for a longitudinal commissure (? muscular), and it is most curious that Sasaki failed to find in *A. pacificus* the "buttons" and "grooves" mentioned by Ijima.

### **Alloposus mollis,** Verrill.

(?) *Haliphron atlanticus*, *Parasira catenulata*, Steenstrup (1860, p. 332).
*Alloposus mollis*, Verrill (1880*b*, p. 394).
,, ,, *id.* (1881, p. 113, Pl. IV, fig. 4, Pl. VIII).
,, ,, *id.* (1881*a*, p. 363).
,, ,, *id.* (1882, p. 366, 420, Pls. L and LI).
,, ,, *id.* (1884, p. 247).
,, ,, Hoyle (1886, p. 73).
,, ,, Joubin (1895, p. 13, Pl. V, VI).
,, ,, *id.* (1895*a*, p. 94).
,, ,, Guerne (1895, p. 109).
,, ,, (?), Joubin (1900, p. 30, Pls. V, XI), (1920, p. 31), Berry (1909, p. 418), Berry (1914, p. 287, text-figs. 11–12), Robson (1926*a*, *passim*), *id.* (1930*b*, p. 397, discussed).

*Type.*—In U.S. Nat. Mus. (*fide* Berry, *l.c.*).

*Specimens seen.*—Fragments in Brit. Mus. and Mus. Océanogr., Monaco.

*Distribution.*—North Atlantic, East: Azores (surface), 37° 10′ N., 11° 48′ W. (surface), 42° 45′ N., 22° 16′ W. (surface), 41° 32′ W. 43° 20′ W. (surface) (Joubin); West: 100–115 miles South of Newport, R.I. (225–487 fms.), off mouth of Chesapeake Bay (300 fms.), S. of Nantucket I.

* Changed to *Parasira* (!) by Steenstrup (1860, p. 333) and subsequently treated (*id.* 1880, p. 104) as a synonym of *Ocythoë*.

(1346–1735 fms.), off Newport, R.I. (506–360 fms.), Martha's Vineyard 310–715 fms.), Delaware Bay (197 fms.) (Verrill); "North Atlantic" (Hoyle): (?) Pailolo Channel, Hawaiian Is. (286–290 fms.) (Berry).

*Description.*—It is not certain that all the complete specimens and fragments of this form which have been recorded under this name are really conspecific. Owing to the fragmentary condition of most of the specimens described, I find it very hard to formulate a description or to discuss the variation. The following description is largely based upon the description and figures of Verrill. It must be understood that the descriptions of the radula, etc., which are due to Joubin and others do not necessarily apply to this species.

The body is ovate and saccular and about as wide as long, the head being rather broader. The eyes are large but scarcely prominent. The arms seem to be in the order 1. 2. 3. 4, and the relative length (variously given) seems on the whole to be rather low, usually under 70%. Verrill originally described the suckers as large and simple, but this is scarcely borne out by his figure (1882, Pl. L, fig. 2) nor by Joubin's figure. Moreover, in both his figures (*l.c.*) Verrill shows the suckers nearly biserial, whereas in Joubin's figure (1895, Pl. VI) they are practically uniserial. In Berry's specimen they seem to be biserial "after reaching the margin of the web." From Joubin's figure of a transverse section (1900, Pl. V, fig. 14) they seem to be fairly thick-walled, but to have little differentiation of the two chambers. In Verrill's figure the web is shown as having the form ABCDE and a maximum depth of about 59%. In Berry's specimen it is shown as deepest laterally, and it is somewhat longer. In Joubin's specimen B (1895) it is very much shallower (*c.* 26%) and not much deeper (viz. 37%) in one of his fragments described in 1900. Verrill (*l.c.*, p. 421) describes the colour (in life) as "pale bluish white speckled with rusty orange-brown chromatophores; inner surface of arms dark purplish-brown; suckers white." Berry does not allude to the oral surface and suckers. His (preserved) specimen had the same general appearance, though the ground-colour was buff.

In Verrill's figured specimens the mantle-aperture is straight and stretches from eye to eye; in Berry's it is sinuous.

Verrill describes the mantle as "united firmly to the head by a ventral and two lateral commissures." The former is no doubt the median adductor; but it is impossible to say what the lateral junctions are. Ijima (in Ijima and Ikeda, 1902, p. 87, footnote) thinks they may be the adhesive-apparatus described by him in *A. pacificus* (*q.v.*), though I cannot help thinking that had there been an adhesive system Verrill would not have used the term "commissures," nor have described them (1882, p. 365) as running "from its [the mantle] inner surface to the basal parts of the siphon." (See p. 219.)

The funnel is deeply sunk in the tissues of the head and projects but little. Its orifice is situated a little beyond the level of the eyes, about a quarter of the way from the latter to the edge of the web in sector E. In Berry's specimen it reaches to nearly half this distance; it is mostly free and prominent and shows a W-shaped funnel-organ.

The mandibles (Joubin 1895) have a very marked subrostral notch. The radula (*id.*, *l.c.*, Pl. V, fig. 11) consists of a tricuspid median, the ectocones of which are large and curved inwards, a bicuspid admedian

with a small ectocone, a second lateral with a long, slanting and weak base, and a second lateral with a characteristic shaft, viz. straight in the basal part and arcuate distally. Joubin figures two marginals, an inner normal one and a rod-like outer one. He may be mistaken about the latter.

The tissues are very gelatinous and their histological structure is described by Joubin (*l.c.*, p. 17) and Tippmar (1913, p. 525).

*Hectocotylus.*—This was described by Verrill (*l.c.*). The modified part has two rows of large suckers and is bordered by fringes of " thin flat lacerate processes." A lateral sperm canal leads into a ligula-like sperm-reservoir (Naef), alongside which is the " penis " (" freier Penisteil," Naef). The arm is developed in a cavity in front of the right eye, and when mature " protrudes from an opening on the inner surface of the web."

*Remarks.*—Berry's specimen being an immature female it is very difficult to say if it is rightly named. Its arms and funnel seem to be longer than in *mollis* and the web of a different shape. The better-defined eyes and the sinuous mantle-edge are additional differentia. It is impossible to speak with certainty of Joubin's specimens. A marked difference in the arrangement of the suckers between Verrill's specimen and specimen A (Joubin 1895) is very noticeable. The great size of this animal is to be noted. One of Joubin's fragments (1920) which was only a small part of the whole was estimated to weigh 20 kilos. His specimen D (1900) had arms well over 5 feet long.

It should be observed that from Verrill's data there must be a good deal of variation in the N. Atlantic *mollis*, *e.g.* the arm-length seems to be about 43% from the 1880 figures and about 72·0% in the 1882 figures.

### **Alloposus hardyi,** Robson.

*Alloposus hardyi*, Robson (1930*b*, p. 397, Pl. IV, fig. 1, text-figs. 17–18).

*Type.*—In British Museum (Holotype).

*Specimen seen.*—The type (♂).

*Distribution.*—R.S.S. " Discovery," Stn. 288, 0° 56′ S., 14° 8′ W., in 0–136 fms. Taken in a young fish trawl.

*Description.*—The body is broadly ovoid and nearly as wide as it is long. It decreases in width from the level of the arms towards the apex. There is a low keel on the left-hand side. The eyes are rather prominent. The arms are in the order 1.2.4.(? 3), 4 being about half as long as the first. The web has the formula ABCDE, E being nearly one-third the depth of A. The suckers tend to be uniserial or very widely alternating except at and just beyond the margin of the web, where they are more or less biserial. They are prominent but small (6·2% of the mantle-length) and have simple undifferentiated cusps. The dorsal surface of the web has become attached to the dorsal surface of the mantle, the visceral mass having undergone a rotation through 60–70° (the oral surface being horizontal).

The pallial aperture is wide and stretches from eye to eye. As in *Alloposina albatrossi*, it is widely **W**-shaped. There is no adhesive-apparatus. The funnel is largely sunk in the tissues of the head, but it has a tubular free portion about 8–10 mm. long. The form of the funnel-organ is unknown. There are 6–7 filaments in each demibranch.

The mandibles are unlike those of *A. mollis* (Joubin, 1895, fig. p. 16) as there is no marked subrostral notch. The radula is like that of *A. mollis* in general (Joubin, *l.c.*, Pl. V, fig. 11), but the form of the first and third laterals are markedly different. I could find no trace of a hectocotylus; but there is a penis with a long diverticle.

*Remarks.*—The species differs from *mollis* (Verrill's description) in (1) its narrower mantle, (2) shape of the pallial aperture and (3) length of the web, and (4) arrangement of the suckers. If Joubin's data are taken as applicable to Verrill's species we must note differences in (1) radula, (2) mandibles, and the length-ration, arm 1 : arm 4. Over and above these differences there is the velar rotation to consider, though we do not, of course, know that this is not an accidental variation.

**Alloposus pacificus,** Ijima.

*Alloposus pacificus*, Ijima (in Ijima & Ikeda, 1902, p. 87, footnote), Berry (1912, p. 397), Berry (1914, p. 288); Sasaki (1929, p. 18, Pl. VIII, figs. 6–8, text-fig. 5).

,, *pelagicus* (in error), Sasaki (*l.c.*, text-fig. 5).

*Type.*—Science College, Tokyo.

*Distribution.*—Misaki, Sagami Prov. (150–200 fms.) (Ijima); Sagami Bay and Awa Prov. (Sasaki).

*Description.*—The following description is based on Sasaki's account (see below).

The body is " campaniform." The head is not demarcated from the mantle-region and the visceral sac is short and very wide, the head being fully one-half of the cephalo-visceral mass and much wider than the body. The eyes seem to be very large, but they protrude very little. The arms are short and in the order 1.2.3.4. The suckers are relatively wide and prominent. They commence in the oral region by being uniserial and assume the biserial condition about the edge of the web, beyond which they seem to be distinctly biserial. The web is of the shape A.B.C = D = E and is about 57% of the arms. The surface of the body is smooth and the tissues are probably subgelatinous. The surface is uniformly covered with large violet-brown chromatophores.

The mantle-aperture is very wide and almost straight. The funnel is nearly all incorporated in the head and has only a small free part. It extends nearly halfway to the umbrella-edge (Sasaki, *l.c.*, text, but cf. fig. 6, Pl. VIII). There is an elliptical olfactory tubercle in the angle of the mantle-aperture.

In his description Ijima says, " there are two buttons at the siphon base fitting into grooves on the inner side of the mantle." I hardly think Ijima could have been in error about this interesting feature, and yet Sasaki makes no allusion to it. Whether Ijima had a particularly well-preserved specimen which subsequently was spoiled by preservation I do not know. At all events Sasaki saw the type-specimen. Neither Ijima nor Sasaki ( ? ) could find any trace of the alleged median and lateral palliocephalic " commissures." The gill has 10 filaments in each demi-branch. The radula has a broad, tricuspid rhachidian with a low central cusp and prominent ectocones. The admedian is rather large with a very

prominent single cusp. The first lateral has a large marginal cusp and its base is sloping and rather triangular, the tooth being midway between the Decapod and Octopod type. The second lateral is straight and has a strong base.

*Remarks.*—This species is distinct from *A. hardyi* in (*a*) depth and shape of the web, (*b*) length of arms, (*c*) bodily proportions, (*d*) details of the teeth, and (*e*) the absence of the dorsal adhesion, and from *A. mollis* in (1) the form of the radula, (2) shape of the mantle and head, and (3) position of the funnel as regards the edge of the web (Verrill's type figure Pl. L, fig. 2).

**Alloposus** (?) sp., Joubin.

" Alloposide mâle," Joubin (1929*a*, p. 14, text-figs. 16–18).

This curious form was obtained by the " Dana " (Stn. 1215 V) off Jamaica, with 322 fathoms of wire out over a very considerable depth. It is represented by a single male specimen 13 mm. in length. It exhibits a highly interesting feature, viz. the union of the base of the funnel with the free edge of the mantle, so as to give rise to a large median orifice and two lateral orifices very much as we find in some Decapoda (see pp. 57 and 215). The specimen had its third right arm highly modified, though Joubin rightly is in doubt as to whether the modification represents an early stage of hectocotylization. The arm consists of a small basal cylinder and a more delicate spoon-like terminal part. As shown by Joubin the organ has a superficial resemblance to the " filament " or " vestigial arms " found in the Vampyromorpha.

2. **Alloposina,** Grimpe, 1922.

(? *Heptapus,* Joubin, 1929.)

The whole mass of the body is compact and globular or ovoid, the arms being very short.

*Type of the genus.—A. microcotyla* (Hoyle, 1886).

*Remarks.*—This group is only known from a single complete description of Hoyle (1904). The specimen seems to differ from *Alloposus* (s.s.) in being globular. As Hoyle's specimen was very small (20 mm. over all) it is very conceivable that it is only a young stage of an *Alloposus.* The hectocotylus is unknown. Joubin's enigmatic *Heptapus* is possibly the same as this form (p. 338).

In 1904 Hoyle referred this form to Steenstrup's *Bolitaena* (p. 326). But there is no doubt in my mind that Hoyle's description (1904) shows that his *Bolitaena microcotyla* is an Alloposid. It is clear that *Alloposus* (*Alloposina*) has nothing to do with *Bolitaena.* The latter was defined, but it was unrecognizable from the description, and no species was cited until after *Alloposus* had been described. Although a species was cited by Hoyle in 1886 for *Bolitaena,* by that time *Alloposus* had been defined and had acquired a type (by monotypy). It must be noted that although Steenstrup had a specimen on which his *Bolitaena* was founded it was not described.

Although there is only one marked difference between *microcotyla* and *Alloposus* (s.s.) I am retaining Grimpe's name for the time being.

**Alloposina albatrossi**, n.n.

Not *Bolitaena microcotyla*, Hoyle (1886, p. 16 [as of Steenstrup MS.]).
*Bolitaena microcotyla*, Hoyle (1904, p. 9, Pl. 3, figs. 6–11, Pl. 4, fig. 1).
*Bolitaena* (? *Alloposus*) *microcotyla*, Robson (1924*a*, p. 671).

*Type.*—In U.S.N.M. (Holotype).

*Distribution.*—Albatross Stn. 3410, off Bindloe Id., 0° 19′ N., 90° 34′ W., in 331 fms.

*Description.*—The following is Hoyle's description (1886) of *B. microcotyla* :—" a soft ovoid body of gelatinous consistency and a reddish-purple colour, somewhat resembling *Cirroteuthis*, but destitute of fins and with the mantle-opening very wide, extending beyond the eyes. . . . The arms are comparatively short and slender, webbed almost up to the extremities and provided with a single row of very small suckers. The jaws are very little curved, and the radula is remarkable in that the rows of teeth present a serial repetition, the fifth resembling the first."

The specimen described in 1904 " resembled a spheroidal mass of jelly barely 2 cm. in diameter." The whole animal seems to have been of an irregularly globular shape, the head and body being indistinguishable one from the other. There is a widely **W**-shaped mantle-aperture. The arms and suckers are not fully described. The arms are in the order 1.2.3 = 4. As the total length is given as 1·8 cm. and that of the first arm as 2·0 cm. (?) it is uncertain what the relative arm-length is. The suckers are more or less uniserial and are 10% of the mantle-length. There is a maximum of 19 suckers. The web is not described. The funnel is broad at the base and rapidly tapers to a prominent and (?) largely free tube. The funnel-organ is **W**-shaped. The olfactory organ is a papilla. The stellate ganglion seems to lie at the termination of the pallial nerve, and is not situated as in the Decapoda and Cirromorpha. There are 6 filaments in each demibranch, or so I infer from the figure and text, which are a little obscure. Hoyle also describes a special cavity produced in the wall of the mantle-cavity which he regards as serving to contain a reserve water supply. This part of his description is very obscure.

The radula has seven rows of teeth. Steenstrup originally stated that there was a serial repetition (as in some Octopodinae), but Hoyle was unable to detect it. The median tooth is normal and like that of other Alloposids. The admedian is bicuspid as in *A. mollis*, the entocone being very much larger than the ectocone. The cusp of the second lateral is heavy and marginal in position. Its base is more *Octopus*-like than is that (*e.g.*) of *A. hardyi*. The ink-sac is present. The colour is not described.

*Remarks.*—Hoyle (*l.c.*, p. 11) says that he compared his Pacific specimen with " one belonging to the same genus in the Hamburg Museum which closely resembles Steenstrup's type of *microcotyla*." It differed in having longer arms, a shorter web and longer funnel. There is evidence that Hoyle saw Steenstrup's type. But one would have expected that he would have compared the Pacific specimen with it more exhaustively. As it is, we now know (p. 326) that *B. microcotyla* is a Ctenoglossate form. As it is necessary to maintain *B. microcotyla*, a new name has to be found for Hoyle's Pacific form.

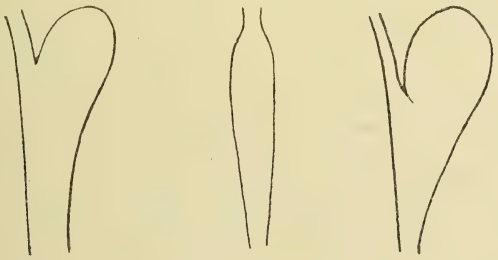
### Tribe 2. Heteroglossa, Naef.

Incirrate Octopods with no apparent sexual dimorphism other than the modification of the third right or left arm as a copulatory organ. The hectocotylus is not autotomous, and consists essentially of a spoon-shaped expansion of the tip of the arm and a lateral seminal channel. The adhesive-organ consists of feeble cephalic and pallial components of which the latter may be absent. The median tooth is usually multicuspid and shows a serial cusp-succession, the admedian is very small and the second lateral has a long base.

In accordance with the conclusions detailed on p. 48, I have included in this tribe the Vitreledonellidae originally part of Naef's Ctenoglossa.

### Family 1. Octopodidae, Orbigny (emend.).

Heteroglossa of shallow- or deep-water habitat. The gills are normally developed and have both inner and outer demibranch. There is a normal, usually well-developed crop. The various ganglia of the "cerebral" complex are highly condensed. The funnel-organ in nearly all species is W- or V V-shaped.



*a* *b* *c*

Fig. 30.—Crop of (*a*) *Benthoctopus berryi*, (*b*) *Bathypolypus arcticus* and (*c*) *Octopus vulgaris*.

The most marked and striking cleavage within the Octopodidae is certainly between the littoral forms and the abyssal. I originally included in the Bathypolypodinae both the highly modified *Bathypolypus* and the less specialized *Benthoctopus* and allied genera. A glance at the table (p. 223) will show, however, that the former are far more evolved and are more like *Thaumeledone*, etc. These highly modified forms are distinguished by the following characteristics.

1. Loss of the ink-sac.
2. Loss or reduction of the crop.
3. Reduction of the gills.
4. Reduction of the radula.
5. Web very deep.
6. Large eggs.
7. Funnel-organ double.
8. Large and wide vagina.
9. Large spermatophores.

Concerning 8 and 9 it is as yet impossible to be certain. From the table it will be seen that the bulk of the characters 1–7 are exclusively

possessed by Nos. 1, 2, 5, 7, 8, 9, 10, 12 and 13. No. 12 has 5 or 6 of the characters cited. Nos. 3, 4, 6 and 11 are imperfectly known, but there are sound reasons for associating them with this group. The residue, however, in no case possess more than four of these characters,

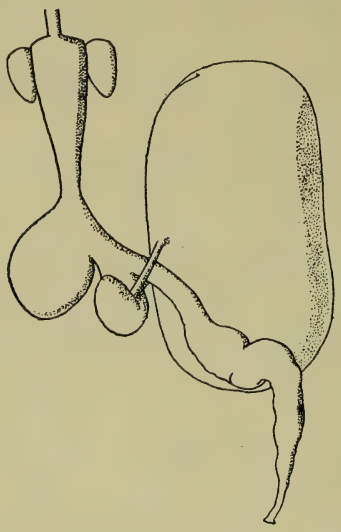


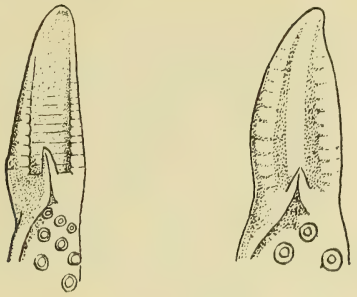
Fig. 31.—*Benthoctopus piscatorum* (Brit. Mus. C. 30). Alimentary canal. × 2·2.

and many of them, though they show one or two " abyssal " characters, nevertheless retain traits that ally them with true *Octopus*. A very real and definite cleavage thus seems to be established, and I believe the less specialized group is more properly retained in the Octopodinae.

Fig. 32.—*Benthoctopus* sp. Radula. × 100.

It remains to ascertain whether all the highly modified abyssal forms should be treated as one subfamily. Now, though *Thaumeledone* and *Bentheledone* agree with *Bathypolypus* in possessing many " abyssal " traits, the two groups are obviously divergent in (i) arrangement of suckers and (ii) radula. The establishment of subfamilies seems to me inappropriate when what we are plainly dealing with is a number of divergent tendencies which have not crystallized out into large and well-defined groups, and when our material and taxonomic data are possibly defective. For the time being I consider it better to refrain from distinguishing among these deep-water forms any groups larger than genera. The family as a whole seems to have diverged along a great variety of lines and with some measure of convergence, but without having given

rise to more clearly-cut and well-defined subdivisions than the two recognized here.



*a* *b*

FIG. 33.—Hectocotyli of (*a*) *Benthoctopus januarii* (× *c.* 3·5) and (*b*) *B. profundorum* (× *c.* 3·75).

| | Ink-sac. | Crop. | Radula. | Mantle-aperture. | Gill filaments. | Eggs. | Web. | Funnel-organ. |
|---|---|---|---|---|---|---|---|---|
| *Bathypolypus* | | | | | | | | |
| 1. *arcticus* | absent | absent | weak | B | 8–7 | ?large | 46–24 | V V |
| 2. *valdiviae* | ,, | ,, | ,, | B | 6 | ? | 41–33 | V V |
| 3. *obesus* | ? | ? | ? | ? | ? | ? | 27 | ? |
| 4. *lentus* | ? | ? | ? | ? | ? | ? | 33 | ? |
| 5. *sponsalis* | absent | absent | weak | B | 7 | large | 33–25 | V V |
| 6. *pseudonymus** | ,, | ? | ? | A–B | 5½ | ? | 35 | V V |
| 7. *salebrosus* (?) | ,, | ? | weak | B, B–C | 9–10 | ? | 33–28 | W, V V |
| *Thaumeledone* | | | | | | | | |
| 8. *brevis* | ,, | present | degenerate | B | 4–5 | large | 68 | 0000 |
| 9. *gunteri* | ,, | absent | ,, | B | 5–6 | ,, | 60 | V V |
| *Bentheledone* | | | | | | | | |
| 10. *rotunda* | ,, | ,, | ,, (?) | B | 4–5 | ,, | 43 | ? |
| 11. ?*albida* | ? | ? | ,, (?) | B–C | — | — | 33 + | V |
| *Graneledone* | | | | | | | | |
| 12. *verrucosa* | ,, | ,, (?) | — | A–B | 7–8 | — | 39–35 | V V |
| 13. *challengeri* | ,, | ,, (?) | weak | B | 5–6 | — | 30 | V V |
| *Benthoctopus* | | | | | | | | |
| 14. *piscatorum* | ,, | present | ,, | wide | 8–7 | large | 31–25 | W |
| 15. *ergasticus* | ,, | ,, | ,, | B | ,, | ? | 28–21 | see text |
| 16. *levis* | ,, | ? | ? | B | 8–8 | — | 43–33 | V V |
| 17. *januarii* | ,, | present | moderate | B | 9–8 | — | 23–22 | — |
| 18. *profundorum* | ,, | ? | = *Octopus* | B ? | 7–6 | — | 34–24 | W ? |
| 19. *abruptus* | ,, | ? | ? | B | 12–10 | large | 24–23 | W |
| 21. *hokkaidensis* | ,, | ? | ? | B, B–C | 12 | ? | 27–24 | W |
| 22. *thielei* | ,, | ? | ? | B | ? | ? | 25 | V V |
| 23. *berryi* | ,, | present | moderate | B, B–C | 8 | ? | 26 | W |
| 24. *sibiricus* | ? | ? | = *Octopus* | ? | ? | ? | ? | ? |
| 25. *eureka* | absent | present | weak | B–C | 8 | ? | 28–23 | ? |
| 26. *lothei* ? | ? | ? | ? | B | ? | ? | 33 | ? |
| *Grimpella* | | | | | | | | |
| 27. *thaumastocheir* | absent | present | ?degenerate | B | 7 | ? | 28 | V V |
| *Teretoctopus* | | | | | | | | |
| 28. *indicus* | ,, | ,, | = *Octopus* | B–C | 10–11 | ? | 40–35 | 0000 |
| 29. *alcocki* | ,, | ? | ? | B–C | 10–11 | ? | 34–29 | 0000 |
| ? *Haptochlaena* | | | | | | | | |
| 30. *chuni* | ? | ? | ? | A ? | 8 | ? | 50 | ? |

* On p. 248 this is treated more correctly as a *Benthoctopus*.

## Subfamily 1. OCTOPODINAE, Grimpe.

For systematic treatment of certain genera see Part I (Robson, 1929).

### **Benthoctopus,** Grimpe, 1921.

Subabyssal Octopodinae devoid of an ink-sac. The mantle-aperture tends to be narrow and the gill-filaments to be reduced in number.

*Type of the genus.—Octopus piscatorum,* Verrill.

**Benthoctopus piscatorum,** (Verrill).

(Figs. 31, 34 & 35.)

*Octopus piscatorum,* Verrill (1879, p. 470).
„ „ *id.* (1880*a*, p. 294).
„ „ *id.* (1882, p. 377, Pl. XXXVI, figs. 1–2).
„ „ *id.* (1882*a*, p. 404, Pl. XL, figs. 1, 1*a*).
„ „ *id.* (1884, p. 248).
„ „ *id.* (1885, Pl. XLII, fig. 5).
„ „ *id.* (1885*a*, p. 563).
„ „ Hoyle (1886, p. 91).
„ „ Lönnberg (1892, p. 8).
Not *Octopus ergasticus,* Fischer (1892, p. 298, as Pfeffer, 1908, p. 20).
*Octopus piscatorum,* Appellöf (1893, p. 3).
*Polypus Normani,* Massy (1907, p. 379).
„ *piscatorum,* Pfeffer (1908, p. 19, figs. 9–10).
„ „ Massy (1909, p. 13, Pl. II, figs. 2–4).
„ „ Russell (1909, p. 446 ?).
„ „ Grimpe (1917, p. 321).
*Benthoctopus piscatorum, id.* (1921, p. 300).
„ „ *id.* (1922, p. 40).
*Polypus piscatorum,* Russell (1922, p. 7, Pl. 2, fig. 7).
*Benthoctopus piscatorum,* Robson (1924*a*, p. 658 and foll.).
„ „ *id.* (1926*a passim*).
„ „ *id.* (1927, p. 254, figs. 2c (as *sasakii*), 3).
„ *sasakii, id.* (*l.c.*, p. 257, figs. 2b (as *piscatorum*), 8).
*Polypus piscatorum,* Grieg (1927, p. 16).
*Benthoctopus piscatorum,* Massy (1928, p. 27).

*Holotype.*—? In U.S. Nat. Mus.

*Distribution.*—(*a*) N.E. America: Le Have Bank, Nova Scotia in 120 fms.; Grand Bank in 200 fms.; 39° 26′ N., 70° 2′ W., in 1362 fms. [about 150 miles S. of Nantucket I.] (Verrill). (*b*) N.W. Europe: 78° 2′ N., 9° 25′ E. [Spitzbergen] 416 fms. (Appellöf); 60° 40′ N., 4° 50′ W. [W. of Shetlands] in 563 fms. (Russell); 61° 27′ N., 1° 47′ W. [N.E. of Shetlands] in 681 fms. (Brit. Mus.); 51° 15′ N., 11° 47′ W. [S.W. Ireland] (Massy) in 710–707 fms.; 66° 41′ N., 6° 59′ E. [Norwegian Sea] in 350 fms. (Appellof); Spitzbergen, from stomach of cod (Grieg); Faeröe Channel in 540–608 fms. (Hoyle).

*Specimens seen.*—Two (♂♀) from the Faeröe Channel (Brit. Mus.); one (♀) from N.E. of Shetlands (Brit. Mus. C. 30).

*Description.*—The body is either globular or ovoid. The head is usually narrower than the body, but in Massy's example it is a little wider. The surface is entirely smooth, though it may show a good many wrinkles produced by preservatives. The arms are short in the type, the British Museum and Massy's specimens, rather longer in those described by Russell. On the average they are about 77% of the total length. The order is irregular, probably 2.1.3.4. The suckers are small, prominent and rather widely alternating. I do not understand why Massy says they are " large " (*l.c.*, p. 14), since she gives the maximum diameter as only 4 mm. Massy notes that the oral surface of the arms is crossed by diagonal ridges as in *O. levis* (Joubin, 1900). I have noticed

this in one specimen, and I think it is probably accidental. Seen in section, the suckers have the circular and basal musculature poorly developed as compared with that of *O. vulgaris*, and the basal chamber is a little larger. There is no marked differentiation in size in the male. The web is moderate to deep (25–31 + %) being moderate in Verrill's specimen (25). It is usually subequal except in the last sector, which is shallower than the others. It is not continued up the arms in the Irish specimen (Massy), but in one of the British Museum specimens (C. 30) a trace of the lateral brachial membrane is found. The funnel is moderately large. In C. 30 it is free for about half its length. The adhesive-organ is weak. Massy, who describes the funnel, does not allude to the funnel-organ. In C. 30 it is not at all well preserved, but it may have been W-shaped. The colour is a dark or light purplish-brown. The peculiar (and distinctive) light area described in the type by Verrill is probably an individual peculiarity. A similar patch (though dorsal in position) was found on the head in *B. berryi* (Robson, 1924*a*, p. 659).

*The radula.*—The rhachidian tooth is multicuspid and may have as many as four cusps a side. The seriation is not easy to make out, though

Fig. 34.—*Benthoctopus piscatorum.* Section of sucker. ×10.

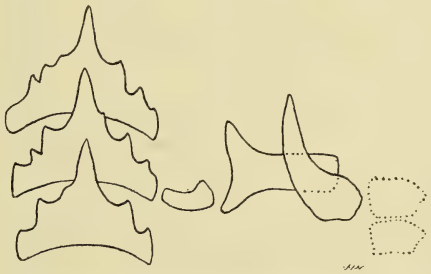


Fig. 35.—*Benthoctopus piscatorum.* Radula. (Fishery Board for Scotland.)

it seems to be more or less asymmetrical. There are about four teeth in a series. These teeth are very broad. In the most unworn teeth of C. 30 the ratio of the base to the height is 7 : 6. The first laterals have low, coarse cusps. The second lateral has a weak cusp and a rather short quadrate base. The third lateral is short and broad-based. Its average width is 25% of its length. Weak marginal plates are found.

*The alimentary canal.*—There is a tolerably well-developed crop. The posterior salivary glands are small and flattish. The stomach and liver are normal. The coecum shows but a faint trace of the spiral condition. The first section of the intestine is thin-walled and is succeeded by a muscular expansion which narrows down to the colon. There is no ink-sac.

*The gills.*—There are 7–8 filaments in each demibranch. The total area of each gill is 10 × 12 mm. The inner filaments are about 75% of the outer in depth.

*The reproductive organs.—Male:* The hectocotylus. The specimen figured by Russell (fig. 7) is tolerably well developed and is about 6·5% of the arm. The sides of the ligula are inrolled, and there is a narrow groove crossed by nine (Massy) laminae. The calamus is short, pointed

and basal. The internal male organs are unknown. *Female:* In the only specimen available the ovary is enormous, measuring 48 × 21 mm. The ovarian eggs measure 13 × 8 mm. The two oviducts are separate almost from their origin, the proximal section is about as long as the distal. The latter have a marked vaginal expansion and very moderate basal ( ? second oviducal gland) swelling. The spermathecae are globular, dark and large (10 × 8 mm.).

*Remarks.*—Verrill's type description is not very exhaustive, and it is not easy to decide if the various European forms referred to the species are correctly diagnosed, and also if *B. sasakii*, Robson, should be treated as a distinct species or only as a subspecies. From the table on p. 74 it will be seen that there are sundry divergences between the various specimens to which the name *piscatorum* has been given. I do not, however, think that they merit subspecific status, though the following points must be noted. It is a little unfortunate that, though Verrill figured the ligula of his species, he did not give the length of the arm so that its relative size might be calculated. (1) Massy's specimen agrees in bodily proportion and arm-length with Verrill's. The suckers are a little larger (index 9·5 as compared with 6·4) and the web shallower. It is otherwise in agreement with the type-description, though the hectocotylus lacks the mid-rib seen in Verrill's figure. (2) Russell's specimens are more globular, the head attains a greater average width (though some of them agree with the type), the arms are somewhat longer and the suckers a little larger. The hectocotylus is much more distinctly grooved. If, however, we regard Massy's specimen as correctly identified, as, in spite of sundry minor divergences, I think we should, it should be noted that its hectocotylus seems to be merely a less developed form of that found in Russell's specimens. (3) Specimen C. 30 (Brit. Mus.) like Russell's is more globular than the type and the web is a little deeper, but it otherwise agrees with the type. (4) The two specimens from the Faeröe Channel, originally described as *piscatorum* by Hoyle and later as *B. sasakii* by myself, certainly constitute a difficulty. Massy examined these and came to the same conclusion as myself, stressing the obvious difference in the size and form of the ligula between them and *piscatorum*. Actually "*sasakii*" differs from the Verrill–Massy *piscatorum* in the following points :—(1) like Russell's specimens and C. 30 it is globular and in one specimen the head is a good deal wider; (2) the suckers are wider (index 11); (3) the hectocotylus is longer (12% as opposed to Massy's 4%), its ligula is deeply excavated and its sides thick and uprolled; (4) the radula differs from that of C. 30 in (i) its narrower rhachidian and (ii) coarser third laterals. It agrees with *piscatorum*, however, in having a smooth surface and short arms. The web, though deeper than that of the type and Massy's specimen, is equalled by that of C. 30. It will be thus seen that Massy's specimen is very like the type, C. 30 and Russell's specimens tend to be more globular, and the latter are longer in the arm. Finally, "*sasakii*," though differing quite markedly from the type, agrees with C. 30 in being globular and having a deep web, and with Massy's *piscatorum* in the one feature in which it differs from the type, viz. the greater size of the suckers. Finally, its ligula, if much larger, is foreshadowed in Russell's specimens. In face of these resemblances I hardly feel justified in retaining *sasakii*

as a distinct species. In my former paper on the subject I figured the female genitalia (*l.c.*, fig. 2, incorrectly as *piscatorum*) and drew attention to the small size of the oviducal gland. Though this statement is correct, I think the size may be due to immaturity. For reasons which are more fully given under *B. ergasticus* I do not agree with Pfeffer's suggestion that the latter should be treated as a synonym of *piscatorum*.

### **Benthoctopus levis** (Hoyle).

(Text-fig. 36.)

*Octopus levis*, Hoyle (1885, p. 229).
,, ,, *id.* (1886, p. 98, Pl. II, figs. 1–4, Pl. III, fig. 1).
,, ,, (?) Goodrich (1896, p. 20).
Not *Octopus levis*, Joubin (1900, p. 35).
,, *Polypus levis*, Thiele (1915, p. 486, Pl. LXXIX).
,, ,, ,, *id.* (1920, p. 435, Pl. LII, figs. 3, 4).
,, ,, ,, Massy (1916*a*, p. 198).

*Holotype.*—In Brit. Mus.
*Specimens seen.*—(*a*) In Brit. Mus.
Two (♂♀) from Heard Id. (Holotype and paratype.)
(*b*) In Indian Museum, Calcutta.
Two (♀♀) from the Indian Ocean.
*Distribution.*—Heard Id., S. Ocean (52° 59′ S., 73° 33′ E.), in 75 fms., on volcanic mud (Hoyle); Gopalpur, Indian Ocean, in 7 fms. (Goodrich); Indian Ocean (where ?) (Massy).

*Description.*—It is not yet certain if the specimens in the Indian Museum attributed to this species are really conspecific. Their measurements are given here collectively with those of the type. They are set out separately in the Table (p. 74).

The body is saccular or ovoid (89, 66), and the head is somewhat narrower than the body. The eyes in the type are prominent, about one-fifth the total area of the mantle. The arms are short, viz. 75 (? 73)–67%. The order of length is very varied. The fourth arm is longest three times in seven cases, the second arm three times. The suckers are small and have an index of 8–6%. They are normally developed in the type and show no discontinuous increase in size. The web seems to have the formula C.B.A. = D.E. (type), or C = D.B.E.A. It is rather deep, being 33–43% of the longest arms.

The surface is quite smooth. The colour seems to be dull grey or slate-blue. Massy notes (*l.c.*, p. 199, footnote) that the slate-blue colour noted "seems like a deposit over a reddish-brown colour." The tissues are firm and muscular. The mantle-aperture is narrow. The funnel is rather small with a short free portion. The cephalic components of the adhesive-apparatus, both in the type and Indian Museum specimens, are practically continuous. The funnel-organ in both the latter is VV shaped. In the type-specimen it is very irregular and its original shape uncertain. There are 8 filaments in each demibranch. In the type the inner demibranch is little reduced, but in one of the Indian Museum examples the reduction is rather marked. There is no trace of an ink-sac in the type and in one of the Indian Museum specimens (the second was not dissected).

*Reproductive organs.*—(1) *Male:* The male organs are only known from those of the type. The hectocotylized arm is 71% of the longest arm. The ligula is about 7% of the arm. The copulatory groove is small but distinct. The laminae are clearly marked and close-set. The calamus is very long, and its apex is more than half-way from the last sucker to the tip of the ligula, a very unusual feature. *Internal organs.* The various parts of the vas deferens are little differentiated. The accessory gland is long and slender. Needham's organ is shorter than the latter (36 : 32); its duct is long. The penis has a longish diverticle. (2) *Female:* In the only dissected female (M. 4761; Indian Museum) the vagina was slender and considerably longer than the oviduct.

*Remarks.*—The specimen from the North Atlantic identified by Joubin as *O. levis* (1900) is certainly not referable to this species. It is discussed (p. 231) elsewhere. I am not altogether certain whether the examples from the Indian Ocean are correctly diagnosed (Massy). Massy's specimen and an additional one found without data in the Indian Museum differ somewhat *inter se*, Massy's specimen being narrower and the other more like the type. In both examples the arms are shorter than in the type, and in the second specimen the web is much deeper than in the latter. Both the Indian Museum examples are females.

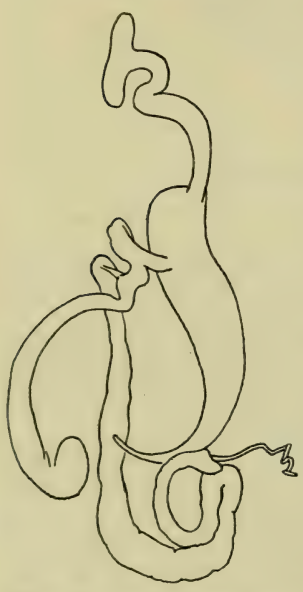


FIG. 36.—*Benthoctopus levis.* Reproductive organs (♂). (Type.)

I think, on the whole, that it is better to leave Massy's identifications mentioned above unchallenged. Actually we require more specimens of this form before we can profitably discuss its variation. Thiele's example from Kerguelen, which I have carefully examined in the Berlin Museum, is certainly not like the type of *levis*, and differs in so many material respects that I have no option but to treat it as a distinct species *B. thielei*, (p. 233).

**Benthoctopus eureka,** Robson.

" *Polypus tehuelchus*, Orbigny," Hoyle (1912, p. 278, figs. 4–5, in error).
*Enteroctopus eureka*, Robson (1929, p. 179, figs. 66–68).
*Benthoctopus eureka*, Robson (1930, p. 331).

This species was fully described by me in Vol. I of this work. It is now necessary to transfer it from *Enteroctopus* to *Benthoctopus*, as on re-examination it has been found to be without an ink-sac. It should also be added that the crop is well developed, the posterior salivary glands are enormous and there are (?) 8 filaments in each demibranch. The species is otherwise very like the other members of *Enteroctopus*, and tends to confirm the impression that some of the *Benthoctopus*-like

forms are local and individual departures from the main *Octopus*-stock and possibly not members of a natural group. The only other noteworthy non-*Octopus* character is the very short second lateral and the generally clumsy and rather undifferentiated character of the radula.

**Benthoctopus berryi,** Robson.

*Benthoctopus berryi*, Robson (1924*a*, p. 658, Pl. II, fig. 7, text-figs. 33–36).
*Octopus berryi*, *id.* (1926*a*, *passim*).
*Benthoctopus berryi*, Massy (1928, p. 90, citation), Robson (1929, p. 41).

*Holotype.*—In Brit. Mus.
*Distribution.*—S.W. of Cape Town in 1200 fms. (Only known from the type-locality.)
*Specimens seen.*—The type.
*Description.*—Only one specimen (a female) of this interesting species is known.

The body is globular and nearly as wide as long (index 93). The eyes are very large (the head being as wide as the body) and prominent and impart to the head the same characteristic shape as that of *Octopus leioderma* (cf. Part I, p. 111). The arms seem to be in the order 1 = 2, 3.4. and to be about 72% of the total length. They are provided with a very narrow ventral membrane. The suckers are small (about 3·2%) and do not increase abruptly on any arm. They do not differ in fine structure from the type found in *O. vulgaris*. The sectors of the web are more or less equal, though E is rather shallower than the others. The maximum depth is moderate (26%). The surface is smooth. The general colour is a light purplish-brown, and is deeper ventrally than dorsally (an unusual feature). In the region of the " neck " it becomes paler, and is lost abruptly in the dorsal and dorso-lateral region just above the eyes. The ocular swellings and the dorsal surface of the umbrella are quite pale, being faintly tinted by sparsely scattered pigment spots. The edge of the web and the arms are darker. The mantle-aperture is moderate (B–C). The funnel is stoutly conical and free for nearly half its length. The siphonal pouches are well developed, but the adhesive-organ is weak. The funnel-organ is very large and **W**-shaped and its four limbs are of equal thickness. The infolding noted on the dorsal edge of the orifice is not (as suggested originally by me) like a valve. It may be of accidental nature.

There are 8 filaments a side in each demibranch. The respiratory surface is distinctly small, being 19% of the mantle-area. The inner demibranch is not much reduced, its main filaments being about 77% of the total depth of the gill. The branchial hearts and branchial gland are well developed.

*The alimentary canal.*—The radula has a multicuspidate rhachidian with asymmetrical seriation. The admedian has a large cusp and shallow base. The second laterals are devoid of an entocone, and the main cusp is marginal. The third laterals are strongly curved. The marginals are degenerate and hardly perceptible. The crop is rather well developed, and is certainly more like that of an Octopodine than that of *Bathypolypus* (see Robson, 1924*a*, text-fig. 35). The stomach is not divided into two

portions as originally stated by me. On opening its cavity, however, the usual grinding apparatus is found (see p. 12). The stomach was full of a mass of comminuted Polychaet remains, the bristles and hooks, which have been identified by my colleague Mr. C. C. A. Monro with those of a sedentary genus. The coecum is large and little twisted. The twist is, however, quite apparent and is more noticeable than in (*e.g.*) *Bathypolypus*. The same tripartite division of the intestine is seen as in *B. piscatorum*. There is no ink-sac.

*Female organs*.—Considering that the animal is large and apparently adult, I was surprised, on re-examining the genitalia, at the minute size of the ovary. The animal measures 47 mm. in mantle-length and may be reasonably thought to be mature. The ovary, however, measures 5 × 4 mm. The oviducts, spermoviducal glands and vaginae are also very small. The oviducts are a third the length of the vaginae.

Rather an outstanding feature is the thinness of the pallial musculature. In no place on the ventral surface does its thickness exceed 1·4 mm. The skin has a subgelatinous quality especially on the arms.

*Remarks*.—It is a pity that this interesting and very characteristic form is known only from a single female. In general facies it recalls *Octopus leioderma* and has something in common with *B. levis* and *piscatorum*, though it is quite clearly distinguished from those forms (see Robson, 1924*a*, p. 662). It seems to be a genuine abyssal form. The fact that its stomach contained only the remains of sedentary Polychaets, is fairly conclusive evidence of its bottom-living habit.

### **Benthoctopus sibiricus**, Løyning.

*Benthoctopus sibiricus*, Løyning (1930, p. 1, Pls. I–II, text-figs. 1–2).

*Type*.—(?) Zoologiske Museum, Oslo. (Holotype, ♂.)

*Distribution*.—76° 12′ N., 146° 10′ E., in 20 fms. (Liakhov Id., New Siberian Is.). From the stomach of a walrus.

*Description*.—This interesting form is unfortunately represented only by the arms and buccal parts, of which the former are incomplete at the tips.

The arms are slender and tapering; their formula cannot be determined. In their present condition they measure, R. 1 = 76, 2 = 84, 3 = 95, 4 = 78; L. 1 = 80, 2 = 76, 3 = 77, 4 = 79. The suckers are alternating. The hectocotylus is small, the ligula being 6% of the total arm-length when measured " from the tip to the distal end of the sperm-groove." This is not exactly the measurement I have regularly used, but it is sufficiently close to mine to make it evident that the ligula is relatively short. The ligula is deeply excavated and without distinct ridges, though the edges are notched and may suggest that ridges were formerly present. The calamus seems to have been prominent. The colour (in alcohol) is dusky grey.

The mandibles are well preserved and apparently strong. The rostrum of the dorsal mandible is about 45% of the total length of the mandible.

The radula consists of about 70 rows. The rhachidians are multicuspidate and asymmetrical, the seriation involving four rows. The

main cusp is about as long as the base is wide. The admedians have an almost straight rectilinear base and a high, rather prominent ectocone. The second lateral has a long and curved base and a deeply indented base line. The teeth on the left side bear a definite endocone, which is entirely absent on the right. This asymmetry is very remarkable, and I know of no similar case in the group. The endocone of the left side is small and situated high up on the main cusp, which there appears to be bifid. The third lateral has a long, rather thick (" slender " (Løyning), but cf. Pl. II, fig. 8*b*) and markedly curved cusp with a small rounded base. The marginal plates are thin, weak and oblong with rounded angles. The ink-sac is unknown.

*Habits, etc.*—Løyning argues on good grounds that this should be a littoral form, as it was taken from the stomach of a walrus shot in a place where the depth of water was about 38 m. and a very great distance from deep water. He points out that the walrus is a markedly stationary form and that the octopod was fairly fresh, so that it is a fair inference that it was taken by its enemy in shallow water.

*Remarks.*—It is very unfortunate that this interesting form is known only from a fragmentary specimen. It is not even certain that it is a *Benthoctopus*, though I think this is likely.

Løyning compares it quite rightly with *B. piscatorum* and the form of the latter which I originally described as var. *sasakii*. Its hectocotylus and radula are suggestive of affinity with these forms. As far as the radula is concerned I do not think that one would hesitate to identify them, except for the remarkable asymmetry of the second lateral mentioned above. The radula is more like that of typical *piscatorum* than that of " *sasakii.*" Løyning stresses its well-developed marginal plates. Actually I have now found better-developed marginals in " *sasakii*," so that the distinction is lessened. The hectocotylus, however, shows more individuality and less likeness to *piscatorum*. The 3rd arm as a whole is longer than its fellows. It is true that the others are nearly all mangled. But $R_1$ is intact and measures 78 as compared with the 95 of $R_3$. In *piscatorum* it is the shortest. The copulatory ridges are very well marked in *piscatorum*, probably absent in *sibiricus*. The calamus is bigger and more prominent in *sibiricus*.

I feel that there is very little as yet to be said concerning this enigmatic form.

(?) **Benthoctopus lothei** (Chun) [? = **B. ergasticus** (Fischer)].

? " *Octopus levis*, Hoyle," Joubin (1900, p. 35, in error), *fide* Grimpe.
*Octopus lothei*, Chun (1914, p. 18, fig. 5).
*Atlantoctopus* (?) *lothei*, Grimpe (1921, p. 300).
,, *pseudonymus*, Grimpe (1922, p. 41).
*Octopus lothei*, Robson (1926, *passim*).
*Atlantoctopus lothei*, Robson (1929, p. 41).

*Type.*—Not traced (? in the Bergen Museum).

*Distribution.*—North Atlantic between Gran Canaria and Cape Bojador (28° 8′ N., 13° 35′ W.), in 1365 m. (746 fms.) (Chun). Only known from the type-locality.

*Description.*—The body is rounded and saccular, rather longer than

wide. The head is just about as wide as the body and is very short. There are no pre- and post-ocular constrictions. The eyes seem to be large and to open in a more dorsal direction than is usual. The arms are in the order 1.2.3.4. and are about 80% of the total length. The suckers are small (6·2%) and only very slightly prominent. The web extends a third of the way up the arms. It is said to broaden a little at the extremities of the first, second and third arms, but this is not apparent in the figure. The mantle-aperture is rather narrow (B) and the funnel inconspicuous. The surface is entirely smooth and of a light greyish-violet colour. The tissues have a " gelatinous " consistency.

*Remarks.*—This form is only known from a single female ( ?) specimen. It was compared with " *Bairdii*," *lentus*, etc., by Chun. Grimpe placed it in his *Atlantoctopus*, and said (*id.*, 1922, p. 41) it was " ev. identisch mit ' Octopus levis Hoyle ' Joubin (1900)," which he had treated as a new species, *A. pseudonymus* (*q.v.*). As elsewhere stated, I see very little grounds for upholding this genus, nor can I see that *lothei* is " evidently identical " with Joubin's form. Neither species is well described, but the general facies is very unlike in the two forms. I believe *B. lothei* may turn out to be a form of *B. ergasticus*, but in the meantime, as the web is deeper and the form of the head and body somewhat different, it is better to treat them as distinct species. Though the ink-sac was not mentioned in the original description, this species is placed in *Benthoctopus* on account of its habitat and general facies.

**Benthoctopus hokkaidensis** (Berry).

*Polypus glaber*, Sasaki (1920, p. 172) (preocc. Wülker, 1920).
,, *hokkaidensis*, Berry (1921, p. 352).
*Octopus glaber*, Robson (1926*a*, *passim*).
*Polypus hokkaidensis*, Sasaki (1929, p. 63, Pls. IV, XI, text-figs. 24–26).
( ?) *Benthoctopus hokkaidensis*, Robson (1929, p. 41).

*Type.*—In U.S. Nat. Mus. (Holotype, ♂.)

*Specimens seen.*—One (♀) from Hokkaido (S. Coast) in U.S. Nat. Museum (No. 332980).

*Distribution.*—Off Hidaka Provinces, Hokkaido (359 and 309 * fms.); off Kinkasan (266 fms.); Suruga Bay (503 fms.).

*Description.*—The body is about as broad as long. Sasaki says (1929, p. 63) that it is " slightly broader than long," without defining his measurements. I find that the (rather distorted) second Hokkaido specimen has an index of about 87%. The range of the width index seems to be about 87–102%. The head is rather narrower than the body (94–82). The neck is weak. The eyes are slightly prominent according to Sasaki. In the specimen that I have seen the eyes, though small, are rather prominent, the animal having a profile very like Berry's *O. leioderma* (1912*a*, Pl. XL, fig. 4). The arms are subequal according to Sasaki. There is, however, from his table a difference of 42 mm. in the arms of No. 1, and comparable differences in the other specimens, so that I do not think we can regard them as subequal especially as the first arm is regularly the longest and appreciably longer than the fourth. The suckers are small (8·6–6·8%) and show no abrupt change in diameter in either sex. The

* In his later account Sasaki gives 303 fathoms.

basal wall of the cup is rather thin and measures about 17–20% of the total diameter. The web is, as Sasaki says, more or less subequal, though he omits the fact that E is regularly shallower than the rest. The depth index is 27–24%, and is on the shallow side. There are tolerably well-developed extensions up the ventral side of the arms. The surface of the body is smooth. Sasaki does not allude to the colour. In the Hokkaido specimen seen by me it is a light purplish-brown. The colour is far deeper in a transverse band just below the eyes and at the edge of the web and on the arms. If this is not due to accident, it is a very rare pattern.

The mantle-aperture is rather narrow (B–C). The funnel is long but nearly completely incorporated in the head, only the tip being free. The siphonal pouches are weakly developed, the adhesive-organ weak. The siphonal area is very characteristic. The funnel-organ is fairly broad-limbed and W-shaped. There are about 12 filaments in each demibranch. The inner filaments show very little reduction. The left gill of the Hokkaido specimen was found to be in an obviously pathological condition, all the filaments being aborted and reduced to stumps. There is no ink-sac.

*The male organs.*—The hectocotylized arm is 75% of the longest arm. The ligula is very short (4·6% of the arm) and cylindrical, with a distinct copulatory groove furnished with about 22 laminae copulatoriae and a minute basal calamus. The internal organs are not very well displayed in Sasaki's figure and cannot be discussed. The penis has a long diverticle which is bent on itself (? by accident) to confer on the whole structure the shape of an S. The vagina and oviduct are " both thin and nearly straight."

*Remarks.*—This form resembles Berry's *Octopus leioderma* in general appearance and sundry other features. They also seem to share the curious feature of having the arms and web darker than the rest of the body. In *hokkaidensis*, however, there is a dark band below the eyes. I have already (1929, p. 112) suggested that *leioderma* is a Bathypolypod. Although the surface, build, funnel-organ, web and hectocotylus are essentially like those of a *Benthoctopus*, the arms are rather short (79–71).

Berry (1921, p. 352) has already pointed out that the name *P. glaber* originally used by Sasaki had been preoccupied by *P. glaber*, Wülker (1920).

There is a discrepancy between my measurements of specimen No. 332980 (U.S. Nat. Mus.) and those given by Sasaki. The individual specimens in his table (p. 64) are not given the registration numbers, but I believe his No. ii is No. 332980. According to Sasaki the maximum arm-length is 127 mm., according to my own it is 155 mm.

### **Benthoctopus thielei,** n. sp.

(Figs. 37–39.)

" *Polypus levis*, Hoyle," Thiele (1915, p. 486, Pl. LXXIX).

(?) *Polypus levis, id.* (1920, p. 435, Pl. LII, figs. 3, 4).

*Type.*—In Zoological Museum, Berlin. (Holotype, ♂.)

*Specimens seen.*—Two (♂♀) from Kerguelen Id. In Zoological Museum, Berlin.

*Distribution.*—Only known from the type-locality, Gazelle Harbour, Kerguelen (Thiele, 1915), and ? from another station on Kerguelen (*id.*, 1920). Both found on the shore (?).

*Description.*—The measurements given by Thiele and those which can be obtained from the figure and from the type do not correspond exactly. Where necessary I give the alternative measurements as well.

The body is rather broadly ovoid in the figure with a width index of 72%. In the type the latter is higher (93%). The head in the figure is about as wide as the body, in the type (80%) and according to the text it is narrower than the body. The eyes are large and prominent. The arms are subequal (in this respect the type and the description agree) and attain a length of 69% (text) or 73% (type). In any case they must be considered as short. The suckers have a diameter index of about 9. The web has the formula C = D, B = E.A, and its sectors may possibly be subequal. It is rather short (25%). The hectocotylized arm of the type is 70% of the longest arm, 66% according to Thiele (text). The ligula in the type and according to Thiele's measurements is 13% of the

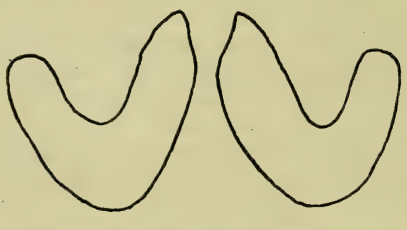


Fig. 37.—*Benthoctopus thielei*. Funnel-organ.
(Type, in Zool. Mus., Berlin.)

arm. In his additional account (1920, fig. 3) Thiele makes the length of the ligula slightly shorter. In the type the ligula is rather pointed, the copulatory groove is sharply and deeply excavated, the laminae are numerous and well seen. The calamus is basal. The organ differs very markedly from that of *levis* (Hoyle, *l.c.*, Pl. II, fig. 2), particularly in the form of the calamus. In his later study Thiele (1920, Pl. LII, figs. 3–4) figured the hectocotylus of what I infer to be the male from Gazelle Harbour. While reproducing the essential features which I noted in the type-specimen it seems to me rather broader and heavier than in the latter. In the slight constriction of the copulatory groove just below the calamus this form of organ reminds one rather of that of *Teretoctopus alcocki*. The penis is short and heavy and it displays a rounded diverticle. I was not able to dissect the internal genitalia out very fully, but examination of the superficial parts revealed the presence of the very large head of a spermatophore (probably of the *ergasticus* type) in Needham's organ.

The funnel-organ is VV-shaped, and there is no trace of an ink-sac.

Thiele (1915) gives a figure in which the colour is reddish-brown, not grey. The skin is smooth.

*Habitat.*—This species is only known from two specimens, one of which was apparently cast up after a storm. The other was from an unknown depth, but probably from shallow water.

*Remarks.*—*B. thielei*, of which only the type-specimen is well preserved, is clearly distinguished from *B. levis*, Hoyle, to which the type was assigned by Thiele, on account of its much shallower web (the proportions of which also differ), longer and differently-formed hectocotylus and its wider suckers.

More specimens of *levis* and *thielei* are required before we can assign them to their correct generic positions. The funnel-organ of *levis* (type)

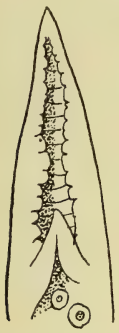


Fig. 38.—*Benthoctopus thielei*. Hectocotylus. (Type, in Zool. Mus., Berlin.)

Fig. 39.—*Benthoctopus thielei*. Penis. (Type, in Zool. Mus., Berlin.)

is unknown. *Levis* (adult) is only known from a single male, and the same is virtually true of *thielei*.

This species may be related to the *januarii-profundorum* group.

**Benthoctopus januarii** (Hoyle).

(Text-figs. 40, 41.)

*Octopus januarii* (pars), Hoyle (1885, p. 229).
„ „ *id.* (1886, p. 97, Pl. VII, figs. 1–4).
Not *O. januarii*, Goodrich (1896, p. 19) (? = *Teretoctopus alcocki*).
? Not *Polypus januarii*, Hoyle (1904, p. 18, Pl. V, fig. 2).
„ „ Berry (1912, p. 392).
„ „ Massy (1916*a*, p. 199).
„ „ Sasaki (1920, p. 172) (? = *B. profundorum*).
*Octopus januarii* (pars), Robson (1926*a*, *passim*).
Not *Polypus januarii*, Sasaki (1929, p. 61, Pls. IV, XI, text-figs. 23–24) (? = *B. profundorum*).
*Benthoctopus januarii* (pars), Robson (1929, p. 41).
Not = "*Octopus levis* Hoyle," var. as Joubin (1900, p. 35).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The holotype.

*Distribution.*—Only known from the type-locality off Barra Grande, N.E. Brazil, in 350 fms. (red mud).

*Description.*—None of the Indian Ocean, Japanese or Pacific specimens attributed to this species are here accepted as correctly diagnosed, and this description is founded on the holotype alone.

The body is globular and widens a little behind the middle line. The

head is considerably narrower than the body (97–68). The eyes, though closely set, are very large, and their antero-posterior axis is nearly half as long as the mantle-length. The total area of a single eye is one-sixth of the total area of the mantle. The arms are in the order 1.2.4.3 or 1.2.3 = 4, and are exceedingly long (87% of the total length). They are slender and finely tapered at the extremities. The suckers are narrow (about 7·3) and are not specially enlarged. The lower wall of the basal cup is moderately thin, but not exceptionally so. The web is of the form A.C.B.D.E., and is about 23–22% of the longest arm, *i.e.* it is quite shallow. There are very feeble brachial membranes up the ventral sides of the arms. The mantle-aperture is rather narrow (B.). The funnel is cylindrical and rather conical at its extremity. It is free for about a quarter of its length. The locking-ridge is subdivided, and there are well-marked parasiphonal pouches. The funnel-organ was not preserved.

The surface is smooth everywhere. According to Hoyle the colour (? in alcohol) is a pale purplish-pink, deeper above than below.

*The alimentary canal.*—The mandibles are normal and like those of an Octopodine. The radula has rhachidia with asymmetrical seriations of type B. 6–7 (Robson, 1925). The first lateral has a narrow base and high

Fig. 40.—*Benthoctopus januarii.* Radula. (Type.)

apparently submedian cusp. The second lateral has a heavy terminal cusp. The third lateral is straight, thick and more expanded basally. The marginals are very degenerate and are quadrangular and oblong. The crop is tolerably well developed and is like that of *B. berryi.* There is no ink-sac.

*The reproductive organs.—Male :* The hectocotylized arm is remarkably short, viz. 58% of the longest arm. The ligula is short (*c.*7% of the arm). Its sides are sharply infolded at the proximal end, and it exhibits a number of faint laminae. The calamus is sharp and prominent, being over one-third of the ligula in length. The sections of the seminal gland are poorly developed. Needham's organ is over six times as long as the penis and much longer (87 : 57) than the accessory gland. There is apparently no appendix. The penis has a moderately long diverticle. The spermatophores are multiple, long and slender.

*Remarks.*—I have had the advantage of seeing the two specimens of Hoyle's *O. januarii* and the four specimens from the Indian Ocean attributed by Massy to this species, together with four other specimens from the Indian Ocean labelled as *O. januarii.* These ten specimens, together with the three described by Sasaki from Japanese waters and the Aleutian Is., constitute a very puzzling and difficult group. The solution offered here may not recommend itself to all students, but in view of the poor

condition of the specimens and other difficulties it seems to me to be the most rational. (*a*) The type of *januarii* (*i.e.* the figured specimen, of which Hoyle gave full measurements) came from Barra Grande, Brazil. It has a globular body which is much wider than the head. The arms are very long (87), the suckers 7·3% of the mantle. The hectocotylus has a narrow oblong ligula. Hoyle associated with this a specimen from east of Japan. The head and body are more of the same width (85 : 69), the arms are shorter (83), the suckers smaller (5·9), the ligula shorter and broader with less incisively marked copulatory groove. The size of the web is more or less the same in the two species, but in the Japanese form C is the deepest sector, instead of A (as in *januarii*). In addition, the internal reproductive organs are remarkably dissimilar. I do not

Fig. 41.—*Benthoctopus januarii*. Reproductive organs (♂). (Holotype.)

think differences of physiological (? seasonal) condition could produce these differences. There can be no other course, then, but to treat Hoyle's Pacific form as a distinct species (*B. profundorum*, *infra*). The only grounds for retaining these highly dissimilar forms under the same name would be the discovery of Japanese or Oriental forms which afford evidence of intermediacy. Neither Sasaki's nor Massy's specimens and data relate to such specimens.

**Benthoctopus profundorum,** n. sp.

(Plate IV, fig. 1; text-figs. 33, 42.)

*Octopus januarii* (pars), Hoyle (1885, p. 229).
,, ,, ,, *id.* (1886, p. 97).
*Polypus* ,, ,, Berry (1912, p. 392).
? *Polypus* ,, Sasaki (1920, p. 172).
,, ,, *id.* (1929, p. 61, Pls. IV, XI, text-figs. 23–24).
*Octopus* ,, (pars), Robson (1926*a*, *passim*).

*Benthoctopus januarii* (pars), Robson (1929, p. 41).
? *Polypus* „ „ Massy (1916*a*, p. 199).

*Type.*—In Brit. Mus. (Holotype.)
*Specimens seen.*—(*a*) In Brit. Mus.
One specimen (♂) from off Yokohama. (Holotype.)
(*b*) In the Indian Museum.
(?) One specimen (♀) from 10° 21′ N., 92° 46′ E. $\left(\text{I.M.M. } \frac{8111}{1}\right)$; (?) one specimen (♀) from the Andaman Sea $\left(\text{I.M.M. } \frac{515}{1}\right)$.

*Distribution.*—Off Yokohama (34° 37′ N., 140° 32′ E.), in 1875 fms. (blue mud) (Hoyle); Bungo Suido (Japan), in 437 fms., off Kii Province, in 600 fms. (54° 33′ N., 178° 44′ E.); Aleutian Is. (54° 33′ N., 178° 44′ E.), in 584 fms. (Sasaki); (?) Andaman Sea (13° 27′ N., 93° 14′ E.), in 405 fms.; same area (10° 21′ N., 92° 46′ E.), in 279 fms. (Massy).

*Description.*—This description is largely founded on the type alone. The status of Sasaki's specimen and those in the Indian Museum is somewhat doubtful. In the description the data for these specimens are given in brackets (I.M. = Indian Museum, S. = Sasaki). The body is of uncertain shape, but was probably broadly ovoid (round, I.M.; subglobular, S.). The head is not so narrow as in *januarii*, its width stands to that of the body as 69 : 85 (62 : 82, 64 : 64, I.M.; 47 : 48, 45 : 41, S.). The eyes though large are smaller than in *januarii*, viz. $\frac{1}{5}$ of the mantle. The arms are probably in the order 1.2.4.3 (1.2.3.4 most frequent, S., ? I.M.), and are 83% of the total length (71–78%, S., 75–82% I.M.). The suckers have an index of 5·9 (5·9–6·7, S., 5·1–6·4, I.M.), and do not show discontinuous enlargement. The suctorial area seems to me to be relatively smaller than is usual in the genus. Otherwise they are normal. The web has the form C.A = B = D.E in the type. E is always the shallowest and C nearly always the deepest. Its maximum depth is 34% (26–24, S.; 34–26, I.M.). The brachial portion is narrow. The surface is entirely smooth. According to Sasaki, it is sometimes of a " purplish-pink," more often darker, deepening to black on the aboral surface of the arms. Neither the type nor the Indian Museum specimens are well enough preserved to allow me to describe the colour. The mantle-aperture in the type is of uncertain extent (?B). According to Sasaki, it is " very narrow." The funnel is conical and free for nearly half its length (short (S.)). The funnel-organ in the type is only very badly preserved. It may have been W-shaped. In Sasaki's specimen it is of the same general shape, but the limbs are noticeably parallel one with another. In the Indian Museum example the organ is more or less obliterated. No. 8111 seems to have a W-shaped organ. The gills have 6–7 filaments in each demibranch in the type, the inner filaments showing marked reduction (60% of the filament). No. 8111 (I.M.) has 8–8 filaments and about the same amount of reduction. In No. 515 the gill is rather larger. It has about 9 filaments; but the amount of reduction is about the same as that in the type. In Sasaki's specimen there are 9–10 filaments. The type and other specimens available are not in sufficiently good condition to justify my examining the alimentary canal. There is no ink-sac in the type or Sasaki's specimen, and in the latter the anal valves are rudimentary. Sasaki figures the radula of one of his specimens.

The rhachidian has an asymmetrical seriation. The first lateral is said to have a minute entocone. The entocone is large and marginal. The second lateral has a heavy cusp and a fairly long base. The third lateral is rather narrow, crescentic and has a wide base.

*Reproductive organs.*—The type is a male. All Sasaki's specimens and both the Indian Museum specimens are females. The hectocotylized arm is very short (60% of the longest arm). The ligula is short (6·9% of the arm) and conspicuously unlike that of *B. januarii* (see fig. 33). The copulatory groove is very weak, and really consists of two parallel grooves which lie on each side of a median ridge. The laminae are only very faintly seen. The calamus is small and sharp.

*Internal organs.*—These are very unlike those of *januarii*. Needham's organ is very short, being little more than twice the length of the penis and shorter than the accessory gland. The common duct enters Needham's organ in a totally different position. The first part of the seminal gland is enormously developed, the later sections only slightly. The penis has a moderately long appendix. The accessory gland is remarkably slender. I do not think the small size of the seminal glands, Needham's organ and the accessory gland are due to physiological causes as the testis, etc., are well developed.

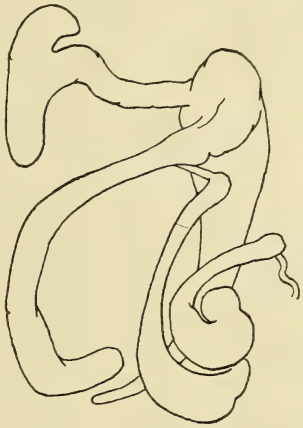


Fig. 42.—*Benthoctopus profundorum*. Reproductive organs (♂). (Holotype.)

*Maximum size.*—290 mm. (type).

*Remarks.*—The relationship of this species, the type of which was originally associated by Hoyle with *O. januarii*, has already been fully discussed (p. 236) and its quite definite and clearly marked differences from that species have been noted (*l.c.*).

Our next concern is with Sasaki's specimens originally identified as *januarii*. These are unfortunately all females, and the single example of *B. januarii* is a male. The arms are much shorter, the gill-filaments somewhat more numerous, and the web a little shallower in Sasaki's example, and sector C is regularly the deepest, not A as in *januarii*. Moreover, the head is as broad as, or broader than, the body. In the radula the form of the admedian and 2nd lateral is different. The individual differences with the exception of that of the head are not very substantial, but I feel that collectively they constitute valid grounds for separating these forms.

There are eight specimens in the Indian Museum referable to this species. Four of these $\left(\frac{515}{1}, \frac{8111}{1}, \frac{1341}{1}, \frac{3348}{1}\right)$ were named *januarii* without any hesitation by Massy, though she noted that the arms are shorter than in that species.

One specimen may be dealt with summarily. This is No. $\frac{350}{1}$, which is so much mangled that it cannot be properly described. The exact form of the funnel-organ is unknown. The hectocotylus is 12% of the arm, and has a very narrow characteristic ligula very unlike that of

*B. januarii* or *profundorum*. Whatever its identity may be, it cannot be associated with either of these species.

As for the rest, I have measured and compared all the specimens carefully and have compared my results with those of Massy. On the whole, our measurements and proportions are in good agreement. I tend to make the suckers a little wider. In one case (No. 8111) I think the web is much deeper than Massy allows. With regard to the funnel-organ, which is of critical importance in this case, Massy very unfortunately examined only two, one of which was in bad condition. As to the other (No. 8111), I agree with Massy as to its form, though it is not in very good condition. It is a great pity that Massy did not examine some of the others, as I would certainly like to have had a confirmation of my results based on fresher material. The first question we have to decide is: are any of the eight specimens in the Indian Museum referable to *B. januarii* or even to *B. profundorum*?

Putting together the series represented by Hoyle's specimen and Sasaki's, we would define the latter as follows:—

| F.O. | Surface. | Width index. | Head index. | Arms. | Suckers. | Web. | Hectocotylus. |
|---|---|---|---|---|---|---|---|
| W | Smooth | 85–71 | 86–69 | 83–71 | 6·7–5·9 | 26–24 | 6·9 |

The only specimens in the Indian Museum series which approaches this are Nos. 515 and 8111. The former is a female and very poorly preserved. The arms are a little longer and the web a little deeper than the above. The funnel-organ is not preserved. The general facies is fairly like that of *profundorum*. No. 8111 has wider suckers and a much deeper web, but it is otherwise not unlike *profundorum*. The structure of the funnel-organ is very uncertain. Massy says, "there is an oval somewhat shield-like median pad and two oblong lateral pads of about half the width of the median one . . . these may have been joined to the median pad."

Nos. 741–742 are not referable to *Benthoctopus* at all. They have a small but distinct ink-sac. The skin is rough, and 742 has a characteristic colour pattern.

Nos. 347, 3348, 1341 all resemble each other in certain important respects, but 347 is much smaller than the other two. They are not in very good condition. They are at once distinguished from the others by (*a*) their large coarse gills, (*b*) the quadripartite funnel-organ (see below), (*c*) the long web (25–34%), (*d*) the narrow head and body, and (*e*) the long hectocotylus (about 16%). It is just possible that No. 350 is referable to this form.

I think it is quite clear that the five differences (which are described more fully on p. 251) above enumerated constitute a very marked departure from our notion of *januarii* as founded on Hoyle and Sasaki's specimens. I have therefore treated them as representing a distinct genus, *Teretoctopus* (p. 249).

Goodrich's Andaman Sea and Bay of Bengal specimens are those herein referred to as Nos. 350 (undiagnosed ? = *T. alcocki*) and 347 (= *alcocki*). Hoyle's *januarii* from the Cocos Id. (E. Pacific) is only known by the radula (Hoyle, 1904, Pl. V, fig. 2), which is by no means satisfactorily drawn. In any case it is unlike that of *B. januarii* (text-fig. 40) and *profundorum* (Sasaki, *l.c.*, text-fig. 23).

In conclusion, I ought to remark that in none of these specimens, except No. 741, is the funnel-organ well preserved. It may be therefore open to question whether the very peculiar quadripartite form seen in Nos. 347, 3348 and 1341 is not purely accidental. The form or its analogues appear in *Thaumeledone* and *ergasticus*, however, and in any case I do not think the form is merely accidental, as the organs do not appear to be seriously damaged.

### **Benthoctopus abruptus** (Sasaki).

(Text-fig. 43.)

*Polypus abruptus*, Sasaki (1920, p. 173).
*Octopus* ,, Robson (1926, *passim*).
*Polypus* ,, Sasaki (1929, p. 68, Pl. VI, fig. 1, text-figs. 29–31).
(?) *Bathypolypus abruptus*, Robson (1929, p. 40).

*Holotype.*—In U.S. Nat. Mus., Washington.
*Specimen seen.*—One (♀, Paratype) from off Kii Province.
*Distribution.*—Off Kii Province, Japan, in 587 fms., with *Opisthoteuthis depressa.* Only known from the type-locality.
*Description.*—The body is " as long as, or longer than, broad " (Sasaki). In the rather distorted paratype it has a width index of 100, and from Sasaki's figures it seems to be 66 in the (larger) male. The head is a little narrower than the body (index in paratype 84), and there is a weakly-marked neck. The eyes are of moderate size and " slightly prominent." The arms are in the order $1 > 2 = 3 = 4$, according to Sasaki. In the female specimen they are in the order 2.3.1.4. Probably they are, as Sasaki says, subequal. They are 82–78% of the total length. In the male the suckers " become abruptly larger to the fourteenth or fifteenth pair " (Sasaki). The fifteenth to seventeenth pairs are greatly enlarged (15% of the mantle-length). In the female there is no abrupt enlargement and the suckers are small and more or less uniform (8%). The basal cup of the suckers is very thin—its wall being barely 1 mm. in thickness. The web which has the formula $A = B = C = D.E$ (type) or $A = D.C = B.E$ (paratype) is rather shallow (23–24%). The brachial membranes tend to be distinctly broad on the ventral side of the arm. The surface of the body is quite smooth, the consistency of the musculature firm (? not gelatinous). The colour of the type is not described; that of the paratype was probably purplish-brown. The mantle-aperture is moderate (B). In the paratype the funnel is distinctly long; but it has only a short free portion (less than one-third of its total length). The funnel-organ is W-shaped, its outer limbs being half as long as the inner.

Fig. 43.—*Benthoctopus abruptus.* Oviduct, etc. × 2.

The gills in the type have 21–23 filaments (10–12 in each demibranch). In the paratype I find as many as 13–14 in each demibranch, a very high number indeed. The total respiratory surface is very large.

Sasaki did not describe the radula and alimentary tract, and I have

not dissected the single specimen loaned by the United States National Museum, beyond making an examination of the anal area. In the latter I could find no trace of an ink-sac. The specimen had been previously dissected, probably by Dr. Sasaki. The latter does not mention the absence of the ink-sac in either of his memoirs, which is a very remarkable omission, seeing that he alludes to its absence in other cases. The anal valves are rudimentary or absent.

*The reproductive organs.*—(1) *Male:* The hectocotylized arm is 73% of the longest arm. The ligula is 7·6% of the arm, narrow and tapering to a point. The copulatory groove is deep and furnished with laminae copulatoriae. The calamus is short and basal. The spermatophores are about 90 mm. long. There is no appendix. From Sasaki's figure (31) the structure of the distal end of the male canal would seem to be remarkable, as the common canal of the spermduct and accessory gland is remarkably long. The penis has a long diverticle.

(2) *Female organs:* The ovary contains eggs which measure up to 12 mm. in length. The oviduct is very short. On the right side of the paratype (on which those organs are intact) the spermoviducal gland is more or less subdivided into two (fig. 43). Sasaki does not mention or figure this. In addition he makes the surprising statement " vaginae thick, short . . ." They are certainly not thick and short in his figure (fig. 29), nor in the actual specimen !

*Remarks.*—Sasaki compares this species with *O. tsugarensis* and *longispadiceus*. The lack of an ink-sac is decisive as to its subfamily position. The lack of other non-Octopodine characters in the structures examined, except perhaps the very small suckers of the female, and its bearing on the systematic position of *Benthoctopus* are discussed elsewhere (p. 51).

**Benthoctopus magellanicus,** Robson.

" *Benthoctopus hyadesii*, Rochebrune & Mabille," Robson (1929, p. 41, not *hyadesii*, R. & M.).
*Benthoctopus magellanicus*, Robson (1930, p. 330, figs. 1–3).
,, ,, *id.* (1930*b*, p. 395).

*Syntypes.*—In M.H.N., Paris (♂♀).
*Specimens seen.*—(*a*) In Brit. Mus.
One (♀) from 49° 00′ S., 61° 58′ W., in 79 fms.
(*b*) In M.H.N., Paris.
The two syntypes.

*Distribution.*—Only known from the type-locality, Orange Bay, S. Patagonia (Mission du Cap Horn) and from north-west of the Falkland Is.

*Description.*—The body is bursiform and about as wide as long. The head is rather narrower than the body (83–78%). The arms are in the order 2.3.1 = 4, and are probably subequal. They are 78–74% of the total length. The suckers are small (13–9·2% of the mantle-length), without discontinuous enlargement. The basal cup is rather thick-walled, its base being 1·7 mm. in thickness. The web has the formula C.B. = A.D.E or B.A.C.D.E. Its formula is 32–31%. The surface of the female is in a very bad condition, but it bears some obsolete warts not unlike those seen in the male. The sides of some of the arms show traces of a definite pustulation. The male, which is in a different state

of preservation, has the skin covered with close-set, irregular, flat prominences which may be actually warts or the product of wrinkling. There are no cirri in either male or female. In both male and female the surface was probably originally of a light purple colour variegated with an irregular dark maculation or reticulation. The mantle-aperture is rather wide. The gills have 9–7 filaments in each demibranch. The inner demibranch is only slightly shorter than the outer. The funnel is small, but prominent and rather pointed in both specimens. In the female the funnel-organ is J L-shaped. In the male it is too badly preserved for study. I believe that in the female the organ is double, but its preservation is not very satisfactory. The crop is very large and *Octopus*-like. There is no trace of an ink-sac in either specimen.

*Reproductive organs.*—The hectocotylized arm is 75% of the longest arm. The ligula is 8·5% of the arm. The calamus reaches to about a third of the distance from the last sucker to the tip of the ligula. Whether the organ was in process of seasonal change or whether it constitutes a new type is uncertain. It is, however, very different from any type known to me in so far as it is, though otherwise fully formed, devoid of a copulatory groove. The longitudinal furrow seen in the drawing is quite superficial. The internal male organs are rather like those of *Benthoctopus eureka.* The distal extremity of Needham's organ is very broad and its proximal end small. There is no appendix penis which occurs in *eureka.* The spermatophores are very numerous and slender. They measure about 52 mm. in length. The penis has a long diverticle.

*Female.*—The ovarian eggs are remarkably long and narrow. They measure 19 × 5·5 mm. The spermoviducal glands are simple and very large. They have been accidentally flattened, but seem to be 16–17 mm. in diameter.

*Remarks.*—In the female specimen the arms are longer than those of the male, and the web-pattern is not the same. In most of the other characters they resemble each other. *Magellanicus* differs from *eureka* in (1) its sculpture, (2) the size of the suckers, arms (the ranges almost overlap), and web, (3) the form of the web, and (4) the lack of a penial appendix. It is, of course, possible that it may be the same as Orbigny's enigmatic *Octopus tehuelchus.* But not only is that species described very inadequately but the web is longer in *magellanicus* and the surface in *tehuelchus* is said to be smooth.

On the strength of an examination of the specimens of "*O. hyadesii*" I placed "*O. hyadesii,*" R. & M., in *Benthoctopus* (1929, p. 41); because neither of the specimens had an ink-sac. On more fully examining the description of *O. hyadesii* (Rochebrune & Mabille (1889, p. H6)) it became immediately clear that the so-called *hyadesii* and its fellow were not to be recognized as such from the description of that species. That description is as follows: " corps ovoïde, couvert de petites verrues et de rides, ces dernières plus particulièrement disposées sur la région antérieure. Tête large, faiblement cubique, à yeux très petits; bras robustes, larges surtout à leur insertion, quadrangulaires, fortement recroquevillés à leur extrémité libre, portant des cupules très rapprochées, en forme d'étoiles; la mem brane de l'ombrelle est à peine visible . . . gris noirâtre sur toutes les régions supérieures, teinté en dessous de gris rougeâtre sale. Long. corps. 0·012; lat. corp. 0·008; long. med. brach. 0·015."

This description is in any case very vague, and the dimensions and the description of the web make it quite impossible to treat the "Cap Horn" Expedition specimens so named (M.H.N., Paris) as referable to it. It is better therefore to retain the name *hyadesii* for the small and probably immature Octopod, the type of which is missing and to describe the adult "Cap Horn" forms under a new name.

I believe that *Benthoctopus magellanicus* and *Benthoctopus eureka* form a special group characterized by the form of Needham's organ, the penis and hectocotylus. The description of the hectocotylus of *eureka* given by me (1929, pp. 180–81) scarcely emphasises sufficiently the shallowness (? absence) of the copulatory groove and the general likeness of the organ to that of *magellanicus*. Into the same group should probably go an unnamed species originally described as *Polypus brucei* by Massy and referred by me as *Enteroctopus* sp. (*l.c.*, p. 181).

The close similarity of these forms with the Magellanic species of *Enteroctopus* makes it very likely that they are derived directly and independently from the latter.

### **Benthoctopus ergasticus** (P. & H. Fischer).

(Text-figs. 44–45.)

*Octopus ergasticus*, P. & H. Fischer (1892, p. 298, text-fig. B).
,, ,, Joubin & Fischer (1907, p. 325, Pl. XXII, figs. 1–4).
*Polypus profundicola*, Massy (1907, p. 377).
,, *ergasticus*, Massy (1909, p. 7, Pl. I, Pl. II, fig. 1).
*Benthoctopus ergasticus*, Grimpe (1921, p. 300).
*Polypus ergasticus*, Robson (1924*a*, p. 668).
*Benthoctopus ergasticus*, Robson (1927, *passim*, figs. 4, 5, 6, 9).
*Octopus ergasticus*, Robson (1926*a*, *passim*).
*Benthoctopus ergasticus*, Massy (1928, p. 27).

*Type.*—(? Syntypes) in M.H.N., Paris.
*Specimens seen.*—(*a*) in Brit. Mus.
Eight specimens (3 ♂, 5 ♀) from S.W. Ireland (1907.12.21.142–148).
(*b*) In M.H.N., Paris.
One (♂) (Syntype ?) from W. Africa.
*Distribution.*—22° 54′ N., 19° 46′ W. (Arguin Bank, W. Africa), in 470–454 m., green sand (Fischer & Joubin); (? Fischer (l.c.), cf. p. 86); S.W. Ireland, loci between 51° 12′–38′ N., 11° 32′–12° 5′ W., in 720–385 fms. (Massy, 1909); 51° 30′ N., 11° 5′ W., in 500–479 fms. (Massy, 1928).

*Description.*—The body is saccular and broad, its width usually little less than its length. Narrower forms are occasionally found, however, the range of variation in this respect being 63–93%. The head is always narrower than the body, sometimes only slightly, sometimes markedly. The "neck" is scarcely apparent. The eyes are large and prominent, and in a specimen 60 mm. long in mantle-length they were over $\frac{1}{5}$ of the mantle-area. The arms are regularly in the order 1.2.3.4 and are 77–87% of the total length. The suckers are very small and are 3·3–8·0% of the mantle-length in diameter. In section they are seen to be tolerably normal. The web is distinctly shallow, and at its deepest is 20–28% of the longest arm. It seems to be in the order ABCDE. The surface in the type-specimen was completely smooth. Massy (1909, p. 7) notes

the occurrence of a few weak tubercles round each eye in her Irish specimens. The colour seems to be a " vinous " red. Massy (*l.c.*) seems to suggest that in the Irish specimens the colour was uniform at least on the body and web. The surface of the body and arms is, as Massy says, soft, but I could discover little indication either of gelatinous tissue or of reduction of the musculature.

The mantle-aperture is regularly narrow (B). The following table shows the variation in this respect :—

| Mantle-length (mm.). | Length from centre of funnel to centre of eye (mm.). | Length from centre of funnel to union of mantle with head (mm.). |
|---|---|---|
| 101 | 40 | 20 |
| 85 | 43 | 20 |
| 88 | 45 | 24 |
| 70 | 42 | 22 |
| 66 | 30 | 18 |
| 58 | 45 | 27 |
| 52 | 28 | 13 |
| 50 (Syntype) | 27 | 13 |
| 48 | 34 | 16 |

It will thus be seen that in one specimen the mantle-aperture extends exactly half-way from funnel to eye; in four it is rather narrower, and in four it is wider.

The funnel is of moderate size and rather broadly conical. The siphonal pouches are present. The adhesive-apparatus is moderate. The funnel-organ is present in the type and in seven out of eight of the Irish specimens. In all of these it is like that shown in Massy's figure, *i.e.* it is double and composed of two solid pads, closely opposed, and somewhat heart-shaped according to Massy. The type-specimen differs from the Irish specimens in having its organ much smaller, though inasmuch as the organ was totally absent in one Irish specimen, I do not consider that this difference is of any significance.

There are 7–8 filaments on an average in each demibranch. The reduction of the inner demibranch is moderate. The largest filaments are from 71% to 83% of the greatest depth.

*The alimentary canal.*—The radula has been figured by Massy (*l.c.*) and myself (1927, fig. 9). Massy shows a unicuspid rhachidian. All the specimens examined by me have 1–3 lateral cusps. Massy's figure is a little obscure as regards the admedian and second lateral. I find that the former has a tall erect cusp. The second lateral is short and weak and approximates to the third lateral in shape far more than is usual in the group. The third laterals (" marginals " Massy) are rather slender and curved. The marginal plates are not mentioned or figured by Massy. There are faint traces of them in one of my specimens.

The two pairs of salivary glands are present and developed to about the same degree as in *O. vulgaris* (Meyer, 1912, fig. 30). The crop is tolerably well developed and rather like that of *B. berryi* (fig. 30*a*). The stomach is rather remarkable. It contains the usual median muscular area, but unlike that of *B. valdiviae* this area (fig. 45) is very thick

and the ridges are scarcely perceptible. It is covered with a thickish chitinous cuticle. The cavity was full of a mass of Polychaet bristles

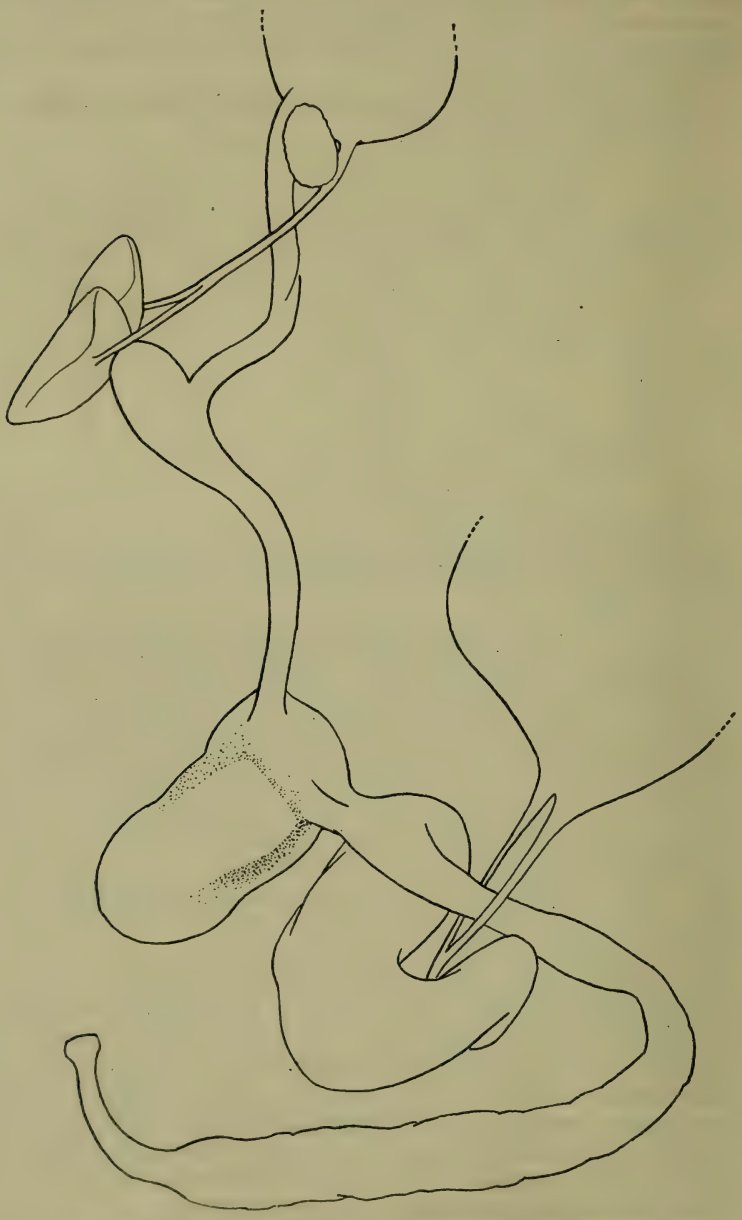


Fig. 44.—*Benthoctopus ergasticus.* Alimentary system. × 3.

which my colleague Mr. C. C. A. Monro has kindly identified as those of a species of Harmothoine Polynoid. The spiral coil of the coecum is plainly seen. The intestine is thin-walled throughout its length except

for a more muscular section near its commencement. There are neither ink-sac nor anal valves.

*Reproductive organs.*—(1) *Male:* The hectocotylized arm is very short, viz. 56–34% of the longest arm. The ligula is 7–13% of the arm. In Massy's first specimen (from S.R. 368) I calculate that the ligula must, on my usual method of measurement (tip of ligula to last sucker), have been 27% of the arm. Either Massy's figures are incorrect or else this is a very remarkable case of discontinuous variation. The ligula is long and pointed, its sides are inrolled, but not solid as in *Bathypolypus*. There are about nine rather strong laminae. The calamus is basal and the area in which the end of the seminal groove terminates is wide and spacious. *Internal organs.* Two of the seminal glands are very well developed. There is a very large appendix (incorrectly shown as small in my figure 5, 1927) and a capacious penial diverticle. The spermatophore is single and of enormous size. (2) *Female:* The vagina is very long and thick (particularly at its proximal end). It is about 80–96% of the total mantle-length. The oviduct proper is exceedingly short (cf. Robson,

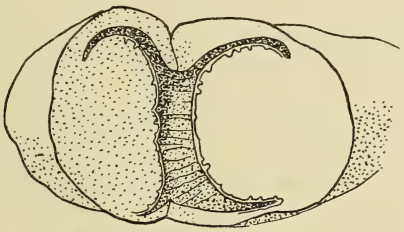


Fig. 45.—*Benthoctopus ergasticus.* Stomach bisected to show thickness of wall.

1927, fig. 6). The spermatheca is small and simple, unless part of the very swollen end of the vagina is part of that system.

*Habits.*—This seems to be an inhabitant of the lower levels of the Continental Shelf. The stomach contents of several individuals were all made up of the remains of sedentary organisms.

*Remarks.*—The identity of this species is well established by the excellent description and figures of Joubin and Fischer. The series of Irish specimens resembles the type-specimen very closely. Indeed, the uniformity in the array before me is very striking. The only marked deviation is seen in the very long ligula of one of Massy's examples (the figures for which may be erroneously given) and in the rather exceptional narrowness of Massy's two examples from S.R. 331 and 363.

As I pointed out in discussing the relationship of this species (1924*a*, p. 668), it is not easy to accommodate in either *Benthoctopus* or *Bathypolypus*, and it seems to me to occupy a position midway between those genera. I think that in the majority of its characters it is more *Benthoctopus*-like. The size and character of the hectocotylus are less like those found most frequently in that genus and the funnel-organ is unique in the subfamily. Though Massy found specimens with unicuspidate rhachidian teeth, while I obtained one from the same material which had a multicuspidate rhachis, I am inclined to disregard this feature.

**Benthoctopus (?) pseudonymus** (Grimpe).

*Octopus levis*, Hoyle, Joubin (1900, p. 35, Pl. III, fig. 7, in error).
*Atlantoctopus pseudonymus*, Grimpe (1922, p. 41).
,, ,, Robson (1929, p. 41).

*Type.*—In Inst. Océanogr., Monaco. (Holotype.)

*Specimen seen.*—The type-specimen.

*Distribution.*—Only known from the type-locality, South of Flores, in 874 fms. (" Princesse Alice," Stn. 719 (1896)).

*Description.*—The body is short and squat, its width exceeding its length. The head is very short and is not demarcated from the body. The eyes are small. The head is about as wide as the body. The arms are in the order 1.2.3.4., but there is little difference between them. The length of the arms is rather uncertain. Measured according to my ordinary method they are 79% of the total length, or, if they are measured from the mouth, 77%. On the other hand, Joubin (*l.c.*, p. 36) gives the proportion as $\frac{1}{1}\frac{2}{?}\frac{4}{8} = 69$. It must be remembered that the type is now more relaxed and the arms may stretch more. The suckers are very small (6·4%). They are rather widely spaced and deeply sunk. In section they are well developed, and the lower wall of the chamber is thick (as in *Octopus*). None of the suckers is specially enlarged. The web is rather deep (33%) and subequal, though sector E is a little deeper than the others. The surface is quite smooth, and was " violacée " (now brownish-purple above and almost colourless below). The mantle-aperture is very narrow (A–B). As in *B. ergasticus*, the width from the middle of the funnel to the junction of mantle and head is about half the distance from the middle of the funnel to the centre of the eye.

The funnel is very small. The funnel-organ is V V-shaped. The gills are relatively very small and have only $5\frac{1}{2}$ filaments in each demibranch.

There is no ink-sac. The female reproductive organs resemble those of *B. arcticus*, though (*a*) the oviduct is longer and (*b*) there is no second spermathecal swelling on the vagina.

*Remarks.*—This form is somewhat of a difficulty. I am compelled to retain it as a distinct species, though it seems to have affinities with *ergasticus* and *piscatorum*.

It is certainly not to be identified with Hoyle's *levis* nor with the Kerguelen form named *levis* by Thiele (p. 233). From the former it is distinguished by (*a*) the bodily shape, (*b*) order of the arms, (*c*) number of gill-filaments, (*d*) proportions of the web, and (*e*) size of the vagina. From the latter it differs in (1) length and shape of the web (though they both agree in the uncommon feature of having the last sector very deep, (2) the size of the suckers, and (3) bodily shape. The funnel-organ, length of the arms, and web, number of branchial filaments and the length of the oviduct differentiate it from *ergasticus*, and the width of the mantle-aperture (Massy, 1909, p. 15), general shape of the web and the number of gill-filaments, and the width of the head and usually of the body (but not always, see Table, p. 74) distinguish it from *piscatorum*. Nevertheless it may be said to have a good deal in common with the last two species, perhaps more with *piscatorum*, and it may be a southern representative

of the latter. Joubin is likewise incorrect in thinking that *O. januarii* is a variety of this form.

At present I can find very little ground for Grimpe's creation of a new genus for this species. This genus has never been properly defined and has depended on the citation of the type. Beyond the enigmatic "considerable development of the arms" (Joubin, *l.c.*, p. 36) at their basal extremity, which might mean anything, there is nothing in the description which can be made the basis of a generic definition. I assume that Prof. Grimpe believed (rightly) that this was a Bathypolypod form and held that it could not be accommodated in any of the available genera. There is some justification for this view, but I think the difficulty is best met by treating the form temporarily as a species of *Benthoctopus*. Its deep web, thick head and body and the form of the funnel-organ suggest that it is nearly related to a form of *Bathypolypus*. On the whole, however, it seems more like *Benthoctopus piscatorum*. It must be borne in mind that the distinction between these genera are difficult to draw.

**Teretoctopus,** Robson, 1929.

Benthoctopodine forms with quadripartite funnel-organ, deep web and short arms. The posterior salivary glands are reduced.

*Type of the subgenus.—T. indicus* (= "*Polypus pricei* Berry," Massy (1916*a*, in error)).

Unwilling as I am to create new generic groups I seem to have no other course open in this instance. The two species placed in this group cannot be very well accommodated in any of the other genera of the Octopodinae. The smooth, narrow body with extremely short arms and deep web, large gill, multicuspid rhachidian teeth and well-developed admedian and second lateral teeth are an assemblage of characters which do not collectively appear in any genus. Even so I would not create a new and distinct group for forms exhibiting a number of characters, which, though forming a novel combination, differ individually from those of allied genera only in relative size. The character of the funnel-organ of the two species dealt with here is, however, so distinctive that they cannot be placed in that group of Octopodinae, viz. *Benthoctopus*, to which they are nearest akin. I regard them as nearer the genus just named than *Bathypolypus*, as (1) the crop is distinct, (2) the radula has a multicuspid rhachis, (3) the body is smooth. The short arms and deep web, however, are more like those of a *Bathypolypus*. It remains to point out that the peculiar type of funnel-organ is found in *Thaumeledone brevis* among the other Octopoda and resembles that of certain Teuthoidea (cf. *Enoploteuthis*).

**Teretoctopus indicus,** Robson.

(Plate III, fig. 2 ; text-fig. 46.)

"*Polypus pricei* Berry," Massy (1916*a*, p. 209, Pl. XXIII, figs. 7–8, in error).

"? *Octopus pricei* (Berry)," Winckworth (1926, p. 326).

"*Polypus pricei* (?)" Robson (1929, pp. 41 and 218–19).

*Teretoctopus indicus*, Robson (1929*b*, p. 608).

*Type.*—In the Indian Museum, Calcutta. (Syntypes.)

*Specimens seen.*—Three (♂) from the Arabian Sea M. $\frac{81\,2\,3\cdot31}{1}$ (Syntypes.)

*Distribution.*—Arabian Sea, 24° 45′ N., 63° 50′ E., in 544 fms. (Massy); ? Pearl Banks, Ceylon.

*Description.*—In the following description I have used my own measurements, which agree very closely with those of Massy. The three specimens are rather small, measuring 25–31 mm. in mantle-length. The mantle is elongate-ovoid and narrow (60–48) with a distinct but very narrow head (40–37) and large prominent eyes. The arms are short, 71–69% of the total length. They seem to be subequal. The suckers are small, widely spaced and prominent. They have an index of 4.4–3.5., and none are especially enlarged. The web is very deep (40–35) and has the formula ?A = B = C = D.E. It has but little extension up the arms, and is peculiarly fragile. The skin is quite smooth. In its present state it is probably more hardened than when Massy described

Fig. 46.—*Teretoctopus indicus* ("*O. pricei*" (Ind. Mus.)). Radula.

it. She commented on its "delicate and fragile appearance . . . so transparent that the venous system can be distinctly traced, without a lens, all about the head and up each arm." She seems to suggest that it is like a pelagic organism. The colour was pale buff with a few large and (?) many small chromatophores. The outer surface of each arm is decorated with two longitudinal rows of alternating chromatophores. The mantle-aperture is wide (B–C). The gills are long and well developed and have 10–11 filaments in each demibranch. The inner demibranch shows some reduction. The radula is well developed. The rhachidian is multicuspid. The cusps are, however, very moderately developed. Without being markedly asymmetrical they have a distinct "lag" on one side. The main cusp is very long in proportion to its base (45 : 31). The admedians have a very prominent cusp and are remarkably wide as compared with the basal width of the rhachis (19 : 31). The second laterals have long bases and strong submarginal cusps. The third laterals are slender with rather small bases. The radula is more like that of *Octopus* than is usual in the subfamily. The crop is rather small, but

of the *Benthoctopus* form. The posterior salivary glands (in two specimens) are singularly small, much smaller than in any form I have examined. The stomach is exceedingly muscular and resembles that of *B. ergasticus* in section, though the muscular mass is deeper and more folded. The intestine is slender, and there seems to be little local dilatation. There is no ink-sac. The funnel and its organ have been described by Massy (*l.c.*, p. 209). The former is very broad at the apex. The organ is composed of four oblong pads, of which the median pair measure 1·50 mm. in Massy's smallest specimen. The *hectocotylus* is 6·3–5·5% of the arm. The latter is 66–59% of the longest arm. The hectocotylus in all the specimens appears to me to be undeveloped. The ligula has a flat, faintly grooved surface and a few faint laminae. The calamus reaches a third of the way along the ligula.

*Habits, etc.*—Massy (*l.c.*) compares the appearance of this form with that of a pelagic organism. It may possibly be of this habit. The stomach is very muscular and the radula is well developed, so that whatever its habitat may be the animal must certainly live on food which requires a good deal of grinding.

*Remarks.*—The status of Massy's specimens has been already discussed (Robson, *l.c.*). I do not think the species can be referred to Berry's species. They have certainly some points in common, and, as far as general build and appearance are concerned, are quite reasonably similar, but the presence of very short arms in *O. pricei*, the form of the funnel-organ (which is somewhat uncertain in *pricei*, but is said by Berry to resemble that of *O. californicus*) and sundry other features, all compel us to differentiate them. *T. indicus* is distinct from *N. alcocki* in the length of the arms, diameter of the suckers, depth of the web and the length and form of the hectocotylus. The latter seem to be undeveloped in all our specimens of *calmani*, but even so it is very unlike that of the smallest *alcocki*. It is very readily distinguished from *B. profundorum* (p. 237).

### **Teretoctopus alcocki,** n. sp.

(Plate III, fig. 3 ; text-fig. 47.)

? *Octopus januarii*, Goodrich (1896, p. 19).
*Polypus januarii* pars, Massy (1916*a*, p. 199).

*Type.*—(Syntypes) in the Indian Museum, Calcutta.

*Specimens seen.*—One from the Andaman Sea (M. $\frac{3\,5\,0}{1}$) (?); one from the Bay of Bengal (M. $\frac{3\,4\,7}{1}$); two from the Gulf of Oman (M. $\frac{3\,3\,4\,8}{1}$, M. $\frac{1\,3\,4\,1}{1}$) (in Indian Museum).

*Distribution.*—(?) Andaman Sea, in 271 fms. (Goodrich); Bay of Bengal, in 193 fms. (Goodrich); Gulf of Oman (Massy), 25° 11′ N., 57° 15′ E., and 23° 46′ N., 58° 31′ E., in 609–700 fms.

*Description.*—I have included in this species two of Massy's *O. januarii* (1916*a*). I have re-measured these and find that my measurements agree fairly closely with Massy's. I utilize my own measurements in this description. The body is elongate-ovoid with an index of 63–55. The head is narrow (51–46) and the eyes large and prominent. The available specimens are very mangled, and the proportions and measurements given are only approximate. The eyes are proportionately to

the body smaller than in *B. januarii* and *profundorum*, viz. one-tenth of the total body-area. The arms are poorly preserved and their order is uncertain. The first is always the largest and attains the length of 76 (? less)–79% of the total length. The suckers are very small (6·6–5·0%) and show no signs of abrupt increase in diameter. The basal portion is moderately thick-walled. The web is rather deep and is 29–34% of the longest arms. The formula is uncertain, A being the deepest sector. The lateral arm-membranes appear to be rather well developed, but of this again I cannot speak with certainty. The surface is in a very bad condition in all the specimens, though I believe it was smooth in the living animal. The original colour is likewise uncertain. The mantle-aperture is rather wide (? B–C). The funnel seems to have been cylindrical and rather broad. The funnel-organ is of the characteristic form already described. It is formed of four small and quite distinct portions, as in *T. indicus* (Massy, *l.c.*, p. 209). In Nos. 1341 and 3348 the patches are subcircular, small and bead-like; in No. 347 they are a little larger and more oblong, and in No. 350, in which they are represented by their scars, they were still larger. In spite of these differences, the systematic value of which we are not yet able to estimate, I think the specimens are referable to the same species. It is noteworthy that Nos. 1341 and 3348, which both come from the Gulf of Oman, have the organ more or less identical, and the rather doubtful Andaman Sea specimen and that from the Bay of Bengal are unlike the Oman specimen and each other. The gills have 10–11 filaments in each demibranch. The gills are remarkably large for a deep-water form. They measure as follows (in mm.) :—

Fig. 47. *Teretoctopus alcocki*. Hectocotylus. × 3·25. (Ind. Mus., 1341.)

| | | | | | |
|---|---|---|---|---|---|
| No. 1341 | 21 × 10 | length | % | mantle-length, | 38% |
| ,, 3348 | 24 × 13 | ,, | ,, | ,, | 40% |
| ,, 347 | 11 × 6 | ,, | ,, | ,, | 40% |

This is in sharp contrast to *B. januarii* and *profundorum* in which the gill is small and does not exceed 25% of the mantle-length. The inner demibranch is substantially reduced. The viscera of all the available specimens are in a very fragmentary condition, and I regretfully abstained from dissecting out the alimentary canal and reproductive organs. There is no ink-sac. The hectocotylus is well preserved in Nos. 1341 and 350 and is alike in both specimens. The arm is 53% of the longest arm in No. 1341 and 59% in No. 350, and is therefore very short as in *B. januarii*. The ligula is, on the other hand, much longer than in that species, viz. about 12% of the arm in No. 350 and 16% in No. 1341. The ligula is long and narrow, and in both specimens its copulatory groove is contracted just above the calamus. The laminae are very much more boldly marked, and unlike *januarii* and *profundorum* the sides of the ligula form an acute angle with the calamus, the base of which they closely enfold, instead of being more or less separated at their bases (Fig. 47).

*Remarks.*—The relationship between this species and *O. januarii* are fully discussed on p. 240. It is distinguished from *B. profundorum* by (*a*) the form of the hectocotylus, (*b*) the deeper web, (*c*) the character of

the funnel-organ, (*d*) the bodily proportions, (*e*) size of the gills and eyes. Further knowledge of the radula, crop, etc., are very much to be desired.

**Grimpella,** Robson, 1928.

The calamus is nearly as long as and deeper than the ligula. The funnel-organ is double. There is no shell-vestige (?). The spermatophores are provided with convoluted upper ends. The web is deep and the radula and alimentary canal show signs of degeneration.

*Type of the genus.—G. thaumastocheir*, Robson.

This genus was founded for the single species *G. thaumastocheir*. The generic characters originally cited are :—(1) the abnormally deep and long calamus, (2) the degenerate adlateral teeth, (3) the double funnel-organ, (4) the long arms and deep web, and (5) the lack of an ink-sac. I stated that, on the whole, the genus was probably more closely related to *Bathypolypus* than to *Benthoctopus*. My intention in framing this definition was to treat the form in question as generically distinct on account of its exhibiting a combination of characters, most of which occurred individually in other genera, as well as one peculiar character, viz. that of the hectocotylus. On reviewing the question and examining other characters as well I conclude that my original view was correct, in that the species cannot be accommodated in any of the other genera. I am inclined to add to the peculiarity of the hectocotylus the general indication of modification in the mandibles, radula and stomach, which, coupled with such knowledge as we possess as to its food, suggest the adoption of a sedentary, débris-eating life. The character of the spermatophores is probably peculiar, though at present this is just a little uncertain. I am less inclined, however, to stress the affinity with *Bathypolypus*. It is probably less closely allied to that genus than to *Benthoctopus*. Actually its chief features may be thus summarized :—

(*a*) Peculiar. i. Hectocotylus.
ii. (?) Spermatophores.
iii. (?) Modification of parts of the alimentary canal.
iv. (?) No shell-vestige.

(*b*) Resemble *Bathypolypus*. i. Funnel-organ.
ii. Sculpture.
iii. General facies.

(*c*) Resemble *Benthoctopus*. i. Length of arms.
ii. Rhachidian tooth.
iii. Crop.
iv. (?) Depth of web.

**Grimpella thaumastocheir,** Robson.

(Plate IV, fig. 2 ; text-fig. 48.)

*Grimpella thaumastocheir*, Robson (1928, p. 108, figs. 1–4).
„ „ *id.* (1929, p. 41).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Only known from the type-locality, Port Lincoln, S. Australia. Depth, etc., unknown.

*Description.*—The body is saccular and flattish. It is as wide as it is long and the interocular width is only slightly less than that of the body (88%). The head is barely distinguishable and the eyes appear small, as they scarcely project at all. They are, however, actually about a quarter of the total area of head and mantle and are therefore rather large. The arms are in the order (?) 2 = 3 = 4.1. and are rather long (82%). The suckers are very large and attain a maximum diameter of 22% of the mantle-length. They exhibit, like other members of the subfamily, a marked increase in size, which attains its maximum diameter at the 9th sucker. The cotyledonary area is wide and shallow and the wall of the basal cup is thin and its musculature seems in places to be penetrated by gelatinous elements. The sectors of the web are subequal and rather deep (30% of the arms). The oral region is very peculiar, being quite horizontal, the bases of the arms rising from it at right angles. As already pointed out (1928, p. 112), this condition might have been produced artificially by the bases of the arms having been tied round a circular block which was then pushed down close to the mouth. I pointed out that (1) the absence of the mark of a ligature on the arms and (2) the probability that the arms would not have retained this posture after the removal of the ligature, are both strong arguments against the artificial origin of this peculiar condition. I have no further evidence on this subject. The arrangement of the bases of the arms, if natural, is certainly without parallel in the order. The surface is covered with rather widely-spaced warts. These are more numerous on the dorsal surface, round the eyes and towards the edge of the web. They tend to fall into two classes—(1) rather large, usually simple, occasionally multifid and conical ones, and (2) smaller, more pustulose ones. The colour was probably purplish-brown, which may have been deeper towards the edge of the web. The body is soft, but I can find no definite trace of an undue amount of gelatinous tissue. As far as I could dissect the pallial area consistently with leaving the animal in a recognizable condition I sought for the shell-vestiges, but could find no trace of them. The pallial aperture is narrow (B). The funnel is remarkably long and slender and its free portion is nearly half its length. The adhesive-organ is weak. There are no obvious parasiphonal pouches. The funnel-organ is double. Its outer limbs are longer than I have shown (Robson, *l.c.*, fig. 3) and are nearly as long as the inner. They are parallel with the latter towards the distal end, and their junction with the median limbs form an acute angle. There are seven filaments a side in each demibranch, the inner series showing very little reduction. The total respiratory surface is 25% of the mantle-area.

*Alimentary canal.*—The lower mandibles are very imperfectly chitinized, and in addition their beaks are simple and very little differentiated. The upper mandibles have a remarkably erect and small beak. The radula has a multicuspid rhachidian, the cusps of which are more or less symmetrically arranged. It is uncertain if seriation occurs in the successive teeth. The first laterals are feeble, the ectocones being very weak. The second laterals have a very prominent heel, their cusps being almost submedian (cf. *Macrochlaena*). The basal plates of these teeth are very shallow. The third laterals have long bases; the shafts are straight and slender, and the points are remarkably recurved so as to be almost hook-

like. The marginal plates are long, narrow and very degenerate. As previously stated (Robson, *l.c.*, p. 113), it would be perhaps inaccurate to say that the radula is degenerate, but it has a general appearance of weakness and fragility which is comparable to that seen in the jaws. Both pairs of salivary glands are present. The posterior pair is of remarkable size, and each member is nearly as large as the liver at least in area. The crop is well developed and is of the *Benthoctopus* type. The stomach is rather thin-walled and its muscular area is, I think, less well developed than usual. This impression of its weakness is borne out by the fact that its contents had a remarkably high proportion of sand granules, which suggests that the animal had been feeding on bottom débris. Polychaet bristles and fragments of Crustacea were also found, but they were not by any means the exclusive contents of the gut, as is so often the case with these animals. There is no trace of the ink-sac.

*Reproductive organs.*—(*a*) The hectocotylized arm is very short, in fact under half the length of the normal arms (48%). The hectocotylus is about 10% of the arm. It is a very remarkable structure and, so far as I know, unique in the order. The calamus is thick, heavy and long,

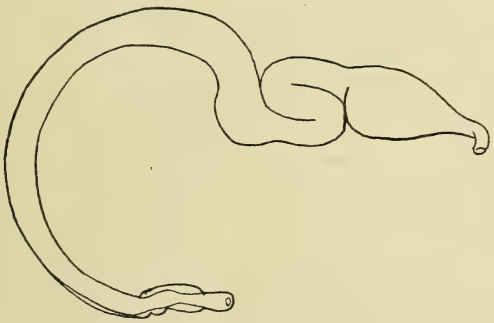


Fig. 48.—*Grimpella thaumastocheir*. Spermatophore. × *c.* 7.

being about three-quarters of the total length of the organ. Its excessive size has caused the ligula to bend downwards so that it lies almost at a right angle to the axis of the arm. The ligula itself is rather slender and pointed, its groove and the laminae being hardly indicated. (*b*) The *internal organs*. The accessory gland is longer than Needham's organ. The penis has a large diverticle and a relatively short free end. Needham's organ contained about four spermatophores measuring about 16 mm. or about $\frac{3}{5}$ of the mantle-length. Only one was obtained in a complete condition. It is (text-fig. 48) of a very remarkable construction owing to the convoluted sperm-tube which also seems to have a stalk-like attachment. One of the fragments of another showed traces of a similar series of convolutions, so that those seen in fig. 48 are probably normal. It is possible that this curious shape is correlated with that of the hectocotylus.

*Habits, etc.*—This little-known and interesting form is recorded as from " Port Lincoln " with no history or further details as to depth, etc. The only clue we have as to the habits, etc., is that afforded by the stomach-contents and the general appearance of delicacy which suggest that the animal is an unaggressive débris-eating form. It is unlikely that it was

taken from deep water, so that any peculiarities it exhibits may be due to adaptation to a muddy habitat.

*Remarks.*—This very interesting form is only known from a single specimen. Its status and relationship are discussed on p. 253.

**Haptochlaena,** Grimpe, 1922.

This genus was proposed by Grimpe (1922, p. 41) without definition for an unnamed *Octopus* referred to by Chun (1914, p. 18) and *Octopus alberti*, Joubin (1895, p. 18, Pl. I, figs. 3–4). Chun's specimen was designated as "*H. chuni* n. sp." by Grimpe in the same work. "*H. chuni*" is "a small flesh-coloured Octopod, in which the eight arms are thrown far back . . . the semi-gelatinous mantle encloses the funnel, only a narrow slit in the mantle being left free, as in the Chiroteuthidae" [sic ! Cirroteuthidae ?]. What exactly Chun meant by "thrown far back" is quite uncertain. He may actually have had before him a form like Joubin's *Retroteuthis* (1929). However, there is no precise description of this singular arrangement, and the only other descriptive item given is that the mantle-aperture is extremely narrow (? type A). Turning now to "*H. alberti*" we find that it is a very young form, measuring only 11 mm. in dorsal mantle-length and 27 mm. over all. Grimpe says of it (*l.c.*) "ev. identisch mit dem vorigen [*H. chuni*]." Why he should have said this when (*a*) the arms are placed normally and not "thrown far back" and (*b*) the mantle-aperture, if narrower than usual, is shown in fig. 4 to be tolerably wide (? B), I do not understand. I have been unable to examine the type of "*H. chuni*," and until it is more fully described, it seems safer to assume that the two forms are not conspecific. *H. chuni* is really undescribed and *H. alberti* is so young that the excellent figures and descriptive data do not assist us to form any idea as to the adult. I have had an opportunity of examining the type in the Oceanographical Museum at Monaco, but beyond ascertaining that the gill consists of 8 filaments, and is of a curious triangular shape and that the pallial element of the adhesive-organ is an elongate ridge (p. 8), I can add nothing to the description. There are, therefore, no adequate grounds on which to found a genus, and while not denying the plausibility of Grimpe's suggestion, I am compelled to treat *Haptochlaena* as of doubtful status. *H. chuni* was obtained in 100 metres (wire) at 37° 37′–42′ N., 29° 18′–25′ W. and *H. alberti* in 43° 53′ N., 9° 1′ W. (Gulf of Gascony) in 250 m. Joubin believes it to have been taken in mid-water. It is very gelatinous and was originally described as an *Alloposus* (Joubin, 1894, specimen B).

**Eledone,** Leach, 1817.

(? *Ozoena*, Rafinesque, 1814; ? *Epistrophea*, Gistel, 1848; *Hallia*, de Rochebrune, 1884; *Hoylea, id.*, 1885.)

Normal littoral Octopodine forms with uniserial suckers and large eggs (about 25% of the mantle-length). The distal suckers on the normal arms are modified in the male, and the hectocotylus is not differentiated into ligula and calamus.

*Type of the genus.—Eledone moschata*, Lamarck.

Two reasons have been advanced for setting aside this familiar name. Hoyle (1901) has proposed Schneider's *Moschites* (1784); but the validity

of this name has, I think, been successfully attacked by Grimpe (1920, p. 206) and myself (1929, pp. 56–7) and does not require discussion. The question has been raised whether *Eledone* is not to be treated as a homonym of the coleopteran genus *Eledona*, Latreille (1796). Cases of this kind are susceptible to much rather fruitless argument. There may be a reasonable objection to the confusion arising out of more or less similar names, and we may invoke etymological evidence to show that *Eledone* is only the Greek form of a Latin *Eledona*. Nevertheless, as long as there is no strict rule to the effect that difference of a single letter is to be disregarded, I think it is better to avoid rejecting a familiar name. Rafinesque's *Ozoena* (1814) certainly has priority and a more serious claim. Rafinesque did not define his genus, but he says definitely " l'*O*[*ctopus*] *moschata* de Lamark [sic] est mon *Ozoena moschata* " (*l.c.*, p. 29). As there is no question as to what Lamarck's species was, there is no doubt that Rafinesque's name should have priority. But I do not think it desirable to reject an old and well-established name and, though I admit that the right of *Eledone* to continue in use is very tenuous, I have retained it pending a decision of the International Commission as to its status as a *nomen conservendum*.

De Rochebrune's *Hoylea* (Hallia) (1884, p. 155, 1885, p. 84) was founded for a large specimen taken off Cherbourg. It had an over-all length of 231+413 = 644 mm. The body was surrounded by a wide web-like peripheral keel. The suckers were in a single row, but irregularly disposed. The arms were 64% of the total length. I think the keel, the short arms and uniserial suckers point unmistakably to *cirrosa*. The body and head are more like those of an *Octopus*, but in *cirrosa* this form is sometimes found (cf. Isgrove, *l.c.*, Pl. I, fig. 1). The web seems low and the first arms remarkably short for *cirrosa*.

In Gray's classificatory scheme (1849) *Eledone* was distinguished as a genus from *Octopus* principally by the fact that the arms have a single row of suckers. Tryon (1879) maintained the groups as separate genera, but made a division within the family according to the number of suckers, *Eledone* and *Bolitaena* being placed in a separate group from the forms with biserial suckers. Joubin (1918*a*, p. 39) maintained this association, but raised the Eledones to the rank of a family which then included

| | | |
|---|---|---|
| Eledonidae : subfamily Eueledonidae [sic]. | | *Moschites* |
| | | *Graneledone* |
| | Bolitaenidae [sic]. | *Bolitaena* |
| | | *Eledonella* |
| | | *Vitreledonella* |

Grimpe (1921) rightly excluded the Eledonellid forms from the Octopodidae altogether, but maintained the distinction between the uniserial and biserial forms as two subfamilies (Octopodinae and Eledoninae). In 1923 (*l.c.*, p. 716) Naef expressed a doubt as to whether the group is a natural and " monotypic " one. He further (*l.c.* footnote) expressed general mistrust of the value of the arrangement of the suckers. For a general discussion on this subject and on the classification of the " Eledoninae " see pp. 51 and foll.

**Eledone moschata** (Lamarck).

(Text-fig. 49.)

*Octopus moschatus*, Lamarck (1798, p. 130).
„ „ *id.* (1799, p. 22).
" Poulpe musqué," Montfort (1802, p. 80, t. XXXIV).
*Sepia moschata*, Bosc (1802, p. 48).
*Ozoena* „ Rafinesque (1814, p. 29).
" le poulpe musqué," Cuvier (1817, p. 363).
*Eledone moschata*, Leach (1817*a*, p. 138).
" *Octopus moschatus* " [of Lamarck], Ranzani (1820, p. 80).
*Octopus moschatus*. Lamarck (1822, p. 658).
„ *moschites*, Carus (1824, p. 319, Pl. 32).
„ *moschatus*, Blainville (1825, p. 365).
(?) „ „ *id.* (1826, p. 190).
*Eledona moschata*, Risso (1826, p. 2).
*Eledone moschatus*, Orbigny (1826, p. 145).
*Octopus* „ Payreaudeau (1826, p. 172).
„ „ (Rafinesque and Lamarck), Blainville (1826, p. 190).
„ „ Sangiovanni (1829, p. 317).
„ „ delle Chiaje (1830, p. 56, "P. muschiato," p. 43).
*Sepia moschata*, Oken (1835, p. 536).
*Eledon moschatus*, Potiez and Michaud (1836, p. 7).
*Octopus* „ Rang (1837, p. 64, t. 91).
*Eledon* „ Orbigny (1840, p. 72, Pl. 1, 1 bis, 3).
*Eledone moschata*, Cantraine (1841, p. 19).
" *Eledone moscata* (e. moschata)," delle Chiaje (1841, p. 5, Pl. V, fig. 1).
" *Eledone moschata* (e moscata)," *id.* (1841*a*, p. 66).
*Eledone moschata*, Philippi (1844, p. 202).
„ „ Orbigny (1845, p. 195).
„ *moschatus*, Gray (1849, p. 21).
„ „ Vérany (1851, p. 7, Pls. 4–6).
? *Eledone ambrosiaca* and *Aldrovandi*, Risso (1854, pp. 45, 47, Pls. XXI, XXII).
*Eledone moschata*, Adams (1858, p. 21, t. 1).
„ *Moschata*, Woodward (1866, p. 165).
„ *moschatus*, Targioni Tozzetti (1869, p. 591).
„ „ Tryon (1879, p. 128, Pl. 40, figs. 65, 66).
„ *moschata*, Stossich (1879, p. 158).
„ *moscata* [sic], Tiberi (1880, p. 12).
*Eledona moschata*, de Rochebrune (1884, p. 159).
„ „ Ninni (1884, p. 162).
*Eledone moschata*, Hoyle (1886, p. 15).
*Eledona* „ Locard (1886, p. 1).
*Eledone* „ Posselt (1890, p. 138).
„ „ Kolombatovic (1890, p. 8).
„ „ Carus (1890, p. 461).
„ „ Lönnberg (1891, p. 9).
„ „ Jatta (1896, p. 239, Pls. 3, 7, 26, 27).
„ „ Babor (1902, p. 799).
not „ „ Johansen (1906, p. 299).

*Eledone moschata*, Joubin and Fischer (1907, p. 328).
„ „ Marchand (1907, p. 353, genitalia).
„ „ Zimmerman (1907, p. 293).
? *Moschites cirrosa* (pars), Pfeffer (1908, p. 22, fig. 14).
*Eledone moschata*, Lo Bianco (1909, p. 646).
*Moschites* (*Eledone*) *moschata*, Naef (1912, p. 749).
*Eledone moschata*, *id.* (1916, p. 17).
„ „ Vayssière (1917, p. 123).
*Moschites* „ Berry (1917, p. 12).
? *Moschites moschata* or *cirrosa*, Wülker (1920, p. 52).
*Eledone* „ Naef (1921, p. 538).
„ „ *id.* (1923, p. 717, figs.).
„ „ *id.* (1928, p. 278, figs.).
? *Eledone moschata*, Nielsen (1931, p. 2).

*Type.*—Not traced. (?) Originally in the M.H.N., Paris.

*Specimens seen.*—(*a*) In Brit. Mus.

Four (1 ♂ 3 ♀) from Naples (98.5.21.353–6); one (♀) from "Mediterranean" (67.3.27.8); two (♀) from unknown localities (79.1.20.7 and 68.3.6.67); one (♀) from "Cape of Good Hope" ? (50.12.31.287).

(*b*) In M.H.N., Paris.

Five (♀) from the Mediterranean; one (♀) from Cadiz; one (♀) from the Red Sea.

(*c*) In M.O., Monaco.

Two from the Mediterranean (♀); six (3 ♂ 3 ♀) from unknown locality.

*Distribution.*—Carus (1890, p. 462) gives many localities in W. and C. Mediterranean from Algiers to Spalato and up the Adriatic as far as Venice (Ninni). He gives no records outside the Mediterranean or E. of Spalato. Girard (1893, p. 396) records it from Gibraltar, and Fischer and Joubin (1907, p. 328) from Cadiz. Girard does not give it in his Portuguese list (1889, p. 200) nor in those relating to the Azores and Madeira (1892, p. 210). One would say that in all probability it does not pass westwards much beyond the Straits of Gibraltar. I can find no satisfactory northern records, and Grimpe (1925, p. 9) says it does not occur in Northern waters. There is, however, some doubt about this, cf. Lönnberg (1891) and Nielsen (1930, p. 2). The record from Iceland (Johansen 1906, cited by Bardarson 1920, p. 134) is more probably an error and "*E. cirrosa*" should be read. I can find no mention of it in lists of the eastern parts of the Mediterranean, but there is a specimen from the Red Sea in the Paris Museum, and Wülker (*l.c.*) records a dubious form from the Red Sea, which he is inclined to regard as *cirrosa*. Vertically its range is inconsiderable. Jatta (*l.c.*, p. 242) and Vérany (*l.c.*, p. 10) regard it as an inhabitant of the shallow coastal waters down to 100 m., though Jatta states that it is sometimes taken down to 200 m.

*Description.*—The differences between *E. moschata* and *cirrosa* constitute a very interesting inquiry. As I have not been able to obtain a large supply of *E. moschata* I do not offer the opinion here given as final, though I think it may be correct. In order to obtain a clear and final idea as to the divergence between these two species a statistical analysis of variation in not less than fifty examples of each species should be made. The differences between the species have been discussed by Hoyle (1886,

p. 103), Posselt (1893, p. 138) and Naef (1912, p. 749). I agree with Naef that, although Posselt noticed and accurately described the interesting modifications of the non-hectocotylized arms, he was mistaken in distinguishing *aldrovandi* and *cirrosa*. Naef's views seem to me eminently sound and are here adopted. He distinguishes the species as follows :—

*E. moschata*. The living animal exhales a musk-like odour (see below p. 262) and is of a greyish-brown colour with blackish-brown blotches on the dorsum. The preserved animal is usually dark in colour, and the skin is smooth or wrinkled. There is no peripheral ridge on the mantle. The suckers of the male on the non-hectocotylized arms are converted into two rows of flattish laminae. It occurs in the Mediterranean, where it is common.

*E. cirrosa*. There is no musk-like odour. The living animal is of a bright yellowish-brown with diffuse rust-brown patches on the back. The preserved animal is always pale reddish-brown (?) and almost white ventrally. There is a fine pale ridge round the ventral periphery of the mantle. The skin is usually closely and finely granulate and warty. The suckers on the ends of the non-hectocotylized arms of the male are close-pressed, rather flattened and extended somewhat as cirri, the actual suckers being completely reduced. It occurs in the Mediterranean and Atlantic.

Naef does not seem to have been aware of the remarkable difference in the structure of the spermatophores (Marchand, 1913, p. 186). After a careful study of the material at my disposal I am unable to find any other significant differences, though I have not enough well-preserved specimens to be certain as to the funnel-organ and genitalia of both sexes. As far, then, as my material allows me to discuss the matter I am in agreement with Naef. The differences between these forms are very interesting. To begin with, the males are far more clearly differentiated than the females, not indeed in the hectocotylus itself (which is very alike in the two species), but in the extremities of the non-hectocotylized arms, and still more strikingly in the shape and detailed structure of the spermatophores (Marchand, *l.c.*). I do not know how far Naef's statement (*l.c.*, p. 750) that the peculiar modification of the arms seen in *E. cirrosa* is more frequently observed in the northern forms of that species may be taken to mean that the southern ones are of a more generalized type. Secondly, two of the three other differences that exist between the species and are common to both sexes, are of a rather trivial order and consist of differences of colour and surface-sculpture. The third difference is remarkable, in that it consists of the presence of a feature in *E. cirrosa* which we have come to regard as an adventitious growth-abnormality, viz. the peripheral keel on the body (Robson, 1929, p. 7). Lastly, as far as I can say at present, the species are very distinct even in the Mediterranean and the three characters alluded to above occur regularly correlated in *E. cirrosa*. It must be borne in mind that the males of these species may have distinct habitats. Naef (*l.c.*, p. 750) says the male of *cirrosa* is very rarely obtained and may live in greater depths (?) than *E. moschata*. The females seem to be common enough, though they do not seem to come right inshore to lay their eggs (Lo Bianco, 1909, p. 646). There is a curious difference between these two species which was first noted by delle Chiaje (1841, p. 5). He remarked

" I marinari napoletini lo (*cirrosa*) denominano *polpo asinisco* per la difficile cottura di lui carne, con sapore meno gradevole degli altri polpi." In spite of the presence of the musky odour the " purpo musco " (*E. moschata*) is more eaten than its tougher relation. This observation is confirmed by other observers (Jatta : Lo Bianco).

*E. moschata* has an ovoid and moderately broad body with a somewhat narrower head than *E. cirrosa*. The arms are more or less of equal length. In the female the average difference between the longest and shortest arms is about 15 mm. The longest arms are 76% of the total length (range 81–73%) on the average. The suckers in all the specimens that I have seen are regularly uniserial and in one line, though occasionally a faint inclination to a zigzag pattern is seen. Probably individuals occur in which they regularly alternate. The diameter of the suckers is 11% of the mantle-length on the average. In one of the males I have seen there is a rapid increase up to the eighth sucker, which is 22% of the mantle-length. In section the suckers do not appear to differ materially from those of *Octopus*. The web is about 30% of the longest arms (range 34–29). Its formula is nearly always ABCDE, E being usually shorter than the rest. The skin is more usually smooth, though the action of preservatives evidently causes marked wrinkling. Sometimes, however, a certain amount of granulation occurs. The colour in life is " grau, graubraun bis rotbraun und auf der Oberseite stets von dunklen, sepia-farbigen bis schwärzlichen Augenflecken unterbrochen " (Naef, 1923, p. 718). The preserved animal is almost invariably of some shade of dark grey or greyish-green, though sometimes a brownish or purplish tint persists. The mantle-aperture is moderately wide. The funnel tends to be rather narrow and prominent with a considerable free portion. There is a deep notch in the inferior border. The funnel-organ is, according to Naef (*l.c.*, p. 718) and Jatta (*l.c.*, Pl. 26), W-shaped. Oddly enough, in all my specimens it is \/\/ shaped. The natural conclusion to draw from this is that the organ has become split accidentally at the base of the W. Nevertheless, it is very strange that it should be so symmetrical and occur in so many specimens. Oddly enough, in Jatta's figure (*l.c.*) the lower angles of the W are shown twisted. It is possible that Jatta did not look closely enough and missed a real break. The gills bear 11–12 filaments in each demibranch. On the whole, the gill is longer and shallower than in *Octopus*.

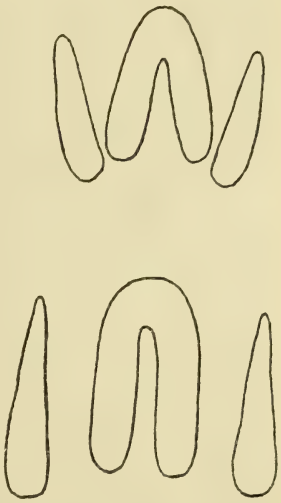


Fig. 49.—*Eledone moschata*. Variation in funnel-organ. (Brit. Mus.)

*The alimentary canal*. (1) The mandibles. Naef (*l.c.*, p. 718) comments on the weakness of the beak in both mandibles, and I can testify to this, as well as to the tendency of the mandible to imperfect chitinization. (2) The radula. The rhachidian (Robson, 1925) has a symmetrical seriation usually of A 2 pattern, though in one preparation at least there are irregularities. In my preparations the mesocone is much longer and

more slender than in Naef's figure (1921, Pl. 16, fig. 4). The adlateral is wide and has a markedly upturned inner ( ? cusp). The second lateral has a pronounced heel and a low, strong cusp. The third laterals are very characteristic in being rather small and strongly curved with wide bases. The marginals are surprisingly long. The heavy, almost triangular third laterals shown by Naef may be accurately represented, but I suspect that the shape is due to their having figured in an unusual orientation. My specimens agree pretty closely with Jatta's figure (*l.c.*, Pl. 26, fig. 6). The anterior and posterior salivary glands are in the same position and of the same size as those of *E. cirrosa* (Isgrove, 1909, Pl. IV). The crop is well-developed and I think it differs from that of *Octopus* in that the crop proper is larger and extends further forward. The stomach and spiral coecum resemble those of *Octopus*. The intestine seems to be longer. The ink-sac is deeply imbedded in the liver. The vascular system has been described by Grimpe (1913).

*The reproductive organs.*—The hectocotylized arm is 60–70% of the longest arm. The modified extremity is very short, 2·8–3% of the arm. I have not seen any trace of the ligula, though Naef (*l.c.*, p. 720) says that it can be made out in well-preserved specimens. The extremities of the other arms are all modified for a distance of 6–15 mm. (G.C.R.), 10 mm. ( ?) (Jatta), 16 mm. (Naef, fig. 430). The modification consists in the subdivision of each of the uniserial suckers so as to form two parallel rows and the antero-posterior flattening of these vestiges, so that each longitudinal series consists of a number of flattish closely-applied plates. The suckers of all the arms in the male are conspicuously enlarged towards the base. This enlargement is not discontinuous. The internal male organs have been described and figured by Marchand (1907). As I have only one male at my disposal I have not dissected it fully. Such examination as I have made shows that the system is very like that figured by Marchand. The accessory gland is short and blunt. There is a well-developed appendix. The various sections of the spermatic gland are thicker and shorter than in *Octopus*. The outstanding difference from the Octopodinae is the fact that there is no penial diverticle. The long, thin penis is a continuation of Needham's organ which is short and stout.

*Female organs.*—These have been described and figured by Brock (1879, p. 96) and earlier writers. The oviducts are longer than is usual in *Octopus*. The vaginae are short and narrow. I have not seen a specimen in which the form of the spermatheca can be satisfactorily ascertained; but from Brock's figure (*l.c.*, Pl. III, fig. 22) it seems to be divided into two parts.

*Cutaneous glands.*—The musk-like odour which is found in this species and apparently in no other Cephalopod is a secretion of the cutaneous glands according to Grimpe and Hoffmann (1926, p. 599). The physiological importance of this secretion is unknown. Grimpe and Hoffmann think it may be utilized as a means of defence. I can find no reference to its chemical composition.

*Habits, etc.*—As far as the Mediterranean is concerned this species seems to prefer living on muddy bottoms at depths rarely exceeding 200 m. (Vérany, Jatta, Lo Bianco). According to Vérany (*l.c.*, p. 10) it is also found on sandy and gravelly bottoms. Risso (1826, p. 2) says it inhabits rocky cavities, but Vérany states that it is rarely taken among

rocks. Lo Bianco emphasizes its preference for muddy areas in the Gulf of Naples. In the latter area it is taken sexually mature from April to July. The eggs, which measure 15 × 4 mm. and are white with a bluish tinge, were noted but once in the Naples Aquarium by Lo Bianco (July). Post-larval stages are found in the Gulf plankton in August till October. Naef (1928, p. 278) was little more successful in rearing the eggs at Naples. The fullest observations are those of Korschelt (1893), which were made at Rovigno. The eggs are 15 mm. long and grouped in twos, threes or fours (cf. *cirrosa*, p. 269) in large clusters. At Rovigno they are found (Naef) in coastal waters attached to stones, empty vessels, etc. Korschelt figures some on the shell of a *Pinna* (see this work, Part I, p. 22). It should be noted that neither Korschelt nor Joubin (1888), who also described the eggs and egg-laying of an *Eledone* at Banyuls, identified their species. The eggs described by Joubin were 7–8 mm. long and are thus smaller than those described by Korschelt as well as those of *cirrosa* (*v.* p. 269). Lo Bianco (*l.c.*) states that from June till August the adults are never caught and only half-grown forms of a maximum length of 20 cm. are obtained. He thinks that it is very probable that during these months, which are conterminous with the [maximum] reproductive activity, the animals are occupied in brooding over the eggs (this operation being well known in other members of the Octopodidae) and are more or less buried on the bottom [!], so that they are not taken in nets. From all accounts *moschata* is an exceedingly common species in the Mediterranean. It appears to live on crabs and Mollusca (Adams, Vérany). Grimpe (1928, p. 363) seems to suggest that it lives exclusively on crabs, when in captivity. Vérany (*l.c.*, p. 11) gives a graphic description of its colour-changes and power of assuming "concealing coloration." He also describes the strength of the siphonal jet and the distance to which it can be projected. Finally he makes the very interesting comment that he kept some out of water for four hours without fatal results. Lo Bianco (*l.c.*) records that a specimen kept in captivity for several weeks devoured five of its own arms. Grimpe (*l.c.*, p. 363) gives a detailed account of its behaviour in captivity mainly in the Naples Aquarium. He notes that it is an annual form, that it will quit its aquarium and try to escape "auf dem Landwege," and that its vitality, as measured by its capacity for standing vivisection is, "erstaunlich gross." It is interesting to note that Grimpe regards *Octopus* as a more phlegmatic animal than *Eledone*, which is "sehr nervos und leicht erregbar."

*Teratology.*—Parona (1900, p. 1) and Vayssière (1917, p. 123) have described specimens of this species with supplementary arms (one extra in each case) due to the dichotomy of a normal arm (see Part I, p. 18).

*Remarks.*—There have been no difficulties as to the application of the name "*moschata.*" The distinction between this species and *E. cirrosa* is discussed on p. 260. The difference between the two species was only slowly appreciated, so that the identity of the various forms described and recorded under this name is no doubt occasionally questionable; but inasmuch as Lamarck alluded to (*a*) the characteristic odour of musk and (*b*) the smooth skin of *moschata* as opposed to the "shagreened" skin of *cirrosa*, the majority of authors have been able to identify this form fairly readily. For the alleged occurrence of *moschata* in Northern waters see p. 259.

**Eledone cirrosa** (Lamarck).

*Octopus cirrhosus*, Lamarck (1798, p. 130).
„ „ „ (1799, p. 21, Pl. 1 & (?) 2).
(?) *Sepia cirrhosa*, Bosc (1802, p. 47).
" Poulpe d'Aldrovande," Montfort (1802, p. 55, Pl. XXXII).
(?) *Ozoena aldrovandi*, Rafinesque (1814, p. 29).
*Octopus cirrosus*, Ranzani (1820, p. 79).
„ „ Lamarck (1822, p. 658).
*Eledone cirrhosus*, Orbigny (1826, p. 146).
*Octopus cirrhosus*, de Blainville (1826, p. 191).
„ *Aldrovandi*, *id.* (*l.c.*).
„ *ventricosus*, Grant (1827, p. 309).
„ *leucoderma*, Sangiovanni (1829, p. 318).
„ *Aldrovandi*, delle Chiaje (1830, p. 57 [P. di Aldrovando, p. 45]).
*Eledon Genei*, Vérany (1837, p. 91, Tav. 1).
*Eledone Pennantii*, Forbes (1838, p. 1).
„ *moschatus*, Orbigny (1840, p. 72, Pls. 1, 1 bis, 3) (pars).
„ *cirrhosus*, *id.* (*l.c.*, p. 79, Pl. 2).
" Eledone Aldrovando (e. Aldrovandi)," delle Chiaje (1841, p. 5, Pl. 6, fig. 5).
" Eledone Aldrovandi (e. Aldrovandiana)," *id.* (1841*a*, p. 66).
*Eledone Pennantii*, MacGillivray (1843, p. 31).
„ *Aldrovandi*, MacGillivray (*l.c.*, p. 32).
„ *Aldrovandi*, Philippi (1844, p. 202).
„ *cirrhosus*, Orbigny (1845 [not 1855 as Naef], p. 194).
„ *moschatus*, Gray (1849, p. 21, pars).
„ *octopodia*, *id.* (*l.c.*, p. 22, ? pars).
„ *moschatus*, Vérany (1851, p. 7, Pls. 4, 5, 6) (pars).
„ *Aldrovandi*, *id.* (*l.c.*, p. 12, Pls. 2, 3).
„ *genei*, *id.* (*l.c.*, p. 15, Pl. 1. As var. of *Aldrovandi*).
„ *cirrhosus*, *id.* (*l.c.*).
„ *cirrhosus*, Forbes & Hanley (1853, p. 211).
„ *Aldrovandi*, & *ambrosiaca*, Risso (1854, pp. 45, 47, Pls. XXI, XXII).
„ *Pennanti*, Fischer (1867, p. 13).
„ *aldrovandi*, *cirrhosus*, Targioni Tozzetti (1869, p. 591).
„ *cirrosa*, Jeffreys (1869, p. 146).
" *Eledone*," Spence Bate (1872, p. 403).
*Eledone cirrhosa*, *moscata*, Sars (1878, p. 366).
*Eledone Aldrovandi* (and var. *genei*), *octopodia*, Tryon (1879, p. 129, Pl. 41).
*Elodone* (sic) *Aldrovandi*, Stossich (1879, p. 158).
*Eledone Aldrovandi* (*Orzoena* [sic]), Tiberi (1880, p. 13).
*Hallia sepioidea*? Rochebrune (1884, p. 156).
*Eledona Aldrovandi*, Rochebrune (1884, p. 159).
„ *Genei*, *id.* (*l.c.*, p. 160).
„ *cirrhosa*, *id.* (*l.c.*, p. 161).
„ *halliana*, *id.* (*l.c.*, p. 162).
*Heledone cirrosa*, Collin (1884, p. 145).
*Hoylea sepioidea*, Rochebrune (1885, p. 85).
*Eledona Aldrovandi*, Ninni (1884, p. 163).
*Eledone cirrosa*, Hoyle (1886, pp. 15, 102).

*Eledone aldrovandi*, (?) *octopodia* and (?) *Hallia sepioidea* Locard (1886, pp. 2–3).
„ „ & *Aldrovandi*, Posselt (1890, p. 138, fig.).
„ *cirrosa*, Norman (1890, p. 468).
„ *Aldrovandi*, & *cirrosa*, Carus (1890, p. 462).
„ *cirrosa*, Lönnberg (1891, p. 8).
(?) *Eledone moschata*, *id.* (*l.c.*, p. 9).
(?) „ sp., Appellöf (1893, p. 6). (See also Friele & Grieg (1901, p. 124).)
„ *cirrosa*, Appellöf (1893*a*, p. 1 (?)).
*Eledone aldrovandi*, Jatta (1896, p. 243, tab. 5, 27, 28, 29).
„ „ Joubin (1895, p. 21).
„ *cirrosa*, Joubin (1896, p. 249).
*Moschites cirrosa*, Hoyle (1902, p. 197).
*Eledone aldrovandi*, Marchand (1907, p. 355).
*Moschites cirrosa*, Pfeffer (1908, p. 22, fig. 14).
*Eledone* [*cirrosa*], Gravely (1909, p. 1).
*Eledone cirrosa*, Isgrove (1909, p. 469 [anatomy]).
„ *Aldrovandi*, Lo Bianco (1909, p. 646).
*Moschites cirrosa*, Massy (1909, p. 16).
„ (*Eledone*) *cirrosa*, Naef (1912, p. 749).
„ *cirrosa*, Naef (1912*a*, p. 197).
*Eledone cirrosa*, Naef (1916, p. 17).
„ *aldrovandi*, Naef (1916, p. 19).
(?) „ *moschata*, Bardarson (1920, p. 134).
„ *cirrhosa*, Joubin (1920, p. 33).
(?) *Moschites cirrhosa*, Wülker (1920, p. 52).
*Eledone cirrosa*, Grimpe (1921, p. 298).
„ „ Naef (1921, p. 538).
*Moschites cirrosa* + var. *zetlandica*, Russell (1922, p. 9, Pl. 1, fig. 2).
*Eledone cirrosa*, Naef (1923, p. 721, text-figs.).
„ „ Nordgård (1923, p. 6).
*Moschites cirrhosa*, Joubin (1924, p. 37).
*Eledone cirrosa*, Grimpe (1925, p. 9, figs. 2–4).
*Moschites cirrosa*, Cuénot (1927, p. 271).
*Eledone cirrosa*, Naef (1928, pp. 279, 281).
„ „ Massy (1928, p. 26).
„ „ Gyngell (1928, p. 216).
„ „ Nielsen (1930, p. 1).

*Type.*—Not traced.

*Specimens seen.*—(*a*) In Brit. Mus.

One (immature) from the Faeröe Channel (1901.8.27.2); one (♀) from the Sound of Sanda (88.3.25.35); one (♂) from St. Andrews (1898.5.21.357); one (♀) from "West of Ireland" (89.9.5.7); one (♀) from "S.W. Ireland" (98.5.21.358); one (♀) from "Irish Coast" (1927.2.4.16); one (♀) from 20 miles off Hook, Co. Wexford (91.6.12.2); three (♀) from Tenby, S. Wales; five (♀) from Plymouth (not registered; 1929.11.13.1–2); two (♂♀) from Naples (1912.8.21.1–2); two (♀) from "the Mediterranean" (67.3.27.6–8); two (♀) from Nice (1889.2.11.4 & 8); two (♀) from unknown localities (79.1.20.8; unregistered).

(*b*) In M.H.N., Paris.

Two from the English Channel (♀); one from Dublin (♀); two from Toulon (♀); one from the Mediterranean; one (♀) from Cherbourg (type of "*Hoylea sepioidea*)."

(*c*) In Mus. Oc., Monaco.

One (♀) from Loch Juadh; one from the mouth of the R. Odet; one from Brest; one from coast of Norway (all ♀); one from unknown locality.

*Distribution.*—(For N. Sea see Grimpe, 1925.) N.W. Atlantic-Mediterranean. S. Iceland (Bardarson, 1920, p. 134, as *E. moschata*). Faeröe Is. (Posselt, 1893, p. 145). Rødøy (N. Norway, 66–67° N.) (Nordgård, 1923). Stoksund and Trondhjem district (*id.*, *l.c.*). Bergen (Posselt, 1893, p. 138). Christiania (Sars, 1878). Askevold, Norway (Joubin, 1920). S. Norwegian Sea (Appellöf, 1893). Göteborg and Bohuslan, Sweden (Lönnberg, 1891). Kattegat (Posselt, 1893, p. 145). Shetland (Jeffreys, Norman, 1890, Russell, 1922). Butt of Lewis (Norman, Hoyle, 1886). Kattegat and Skagerrak (see Grimpe, 1925). Denmark, W. Coast (Posselt, *l.c.*, p. 145). Limfjord (Collin, 1884). Faeröes (Nielsen). Faeröe Channel (Brit. Mus., ? Hoyle, Russell, 1922, var. "*zetlandica*"). The Minch (Russell, *l.c.*, var. "*zetlandica*"). West of the Orkneys (*id.*). Scotland, Lamlash, St. Andrews (Norman, *l.c.*). Aberdeen (MacGillivray, 1843). Moray Firth, Firth of Forth, Dornoch Firth (Russell, 1922). Loch Juadh (Joubin, 1920). Isle of Man (Forbes, 1838). North Sea (Russell, *l.c.*, Grimpe, 1925 (full bibliography), Gyngell, 1928). England and Wales:—Pt. Erin (Gravely, Isgrove). Plymouth (Brit. Mus.). "S. Devon" (Spence Bate). Tenby (Brit. Mus. see Jeffreys and Alder and Hancock). Ireland:—Wexford (Hoyle, 1886), "all parts of the Irish Coast" (Massy, 1928, p. 26, see also *ead.* 1909). S. Ireland (Joubin, 1920). France, N. and W. (Locard, 1886). France, Cherbourg (Fischer, 1867). Bay of Biscay (Joubin, 1895, 1896). Brest (Joubin, 1920). Mouth of the Odet (*id.*, *l.c.*). Arcachon (Cuénot, 1927). Mediterranean, (Auctt.) as far East as Lissa and Lesina in Dalmatia (Gray, Kolombatović) Dalmatia (Gray). S. end of Adriatic, but not North (Ninni). Naef considers that the eggs described by Korschelt (*v.* p. 263) from Istria (Rovigno) are those of *moschata*. Wülker (1920, p. 52) hazards that a specimen from the Red Sea may be *cirrosa*. The species is not recorded from more northern localities and just seems to pass the Arctic Circle. It does not occur, *e.g.*, in Deriugin's Kola Sea list (1915), in Odhner's (1915) and Grieg's Spitzbergen lists (1927) and Posselt's fauna of Greenland (1899). It is given at Ostroumov's Station 31 (1896, p. 74) in the Sea of Marmora, but not in Forbes' Aegean list (1844, p. 131) nor in von Martens' Black Sea list (1874). Grimpe (1925, p. 9) says "Ostroumov's Angabe . . . ist wertlos, da russisch" [!]. Certain records of juvenile forms (*e.g.* Appellöf (1893), Friele and Grieg (1901)) are uncertain, but may be referable to *cirrhosa*. For a detailed discussion of the North Sea records see Grimpe (*l.c.*, p. 9). In the S. English Channel it is usually more common than *Octopus*, a fact observed in 1872 by Spence Bate (*l.c.*).

*Vertical range.*—Jatta gives the maximum depth as 200 m.; Massy gives a maximum of 461 fms. in 51° 25′ N., 11° 37′ W. and one taken at 250 fms. in 50° 18′ N., 11° 5′ W. Russell (1922) gives a maximum of 464 fms. Grimpe has two records of specimens taken at "400 m. line" (Shetlands and Stavanger). The above-mentioned young specimen (Appellöf (1893), Friele and Grieg (1901)) from 63° 5′ N., 0° 53′ W. came

from 587 fms. The majority of the records are of much shallower depths. If we may trust Vérany's observation (1851, p. 14) it seems to replace *E. moschata* in deeper water and further from the coast. Joubin (1895) records a young specimen taken in 155 m. 135 kilometres from the coast.

*Description.*—(For difference between this species and *E. moschata* see p. 260.) The body is ovoid and moderately broad. The head is narrower than the body. The arms are about equal in size and are somewhat shorter on the average than those of *E. moschata*, viz. 73% (range 67–81). The suckers have an average diameter of 12·8% of the mantle-length. In the two males which I have seen the enlarged suckers do not exceed the average for females. The suckers are uniserial in all the specimens which I have seen. Gravely (1909, p. 6) and Chadwick (in lit., Gravely, *l.c.*, p. 7) record a well-marked zigzag or almost biserial arrangement. Neither Naef nor Jatta allude to important deviations from this arrangement. In section there seems to be no difference between the suckers of this species and *E. moschata*. The web is about 29% (21–41% in adult) of the longest arms. I think the formula may be written as A = B = C.D.E, E usually being quite definitely shallower than D. The skin is covered with fine and usually close granular warts. Joubin (1920) alludes to one specimen as remarkable on account of its "villosités." Among these are usually larger warts and over each eye is a single cirrus. The sculpture may in exceptional cases be almost completely erased from the surface. The living animal is a yellowish- or reddish-orange to reddish-brown dorsally. Ventrally it is paler and may show a greenish iridescence. The preserved specimens are usually a pale reddish-brown above, pale yellow below. For a good description of the colour and colour-changes in northern *cirrosa*, see Isgrove (1909, p. 478). Round the periphery of the mantle is regularly seen a fine low ridge ("Seitenlinie"). In seventeen specimens which I have seen the ridge is present and well developed in fourteen, in two it is seen on one side only, and in one it was very weak. (For the significance of this ridge see Part I, p. 7.) Isgrove (*l.c.*), who worked on specimens from Plymouth and Port Erin, does not comment on the ridge. The mantle-aperture is moderately wide (B–C). The funnel is less cylindrical than that of *E. moschata*, and it also tends to be more involved in the tissues of the head. The funnel-organ is W- or Ꮤ-shaped. I am a little uncertain as to any differences that may occur between the two species in this organ. In northern *cirrosa* I find the outer arms more pointed. Jatta (*l.c.*) shows the organ of *cirrosa* as broader and coarser than that of *moschata*, and I am inclined to agree with this. The gills have about 11 filaments in each demibranch. The gill as a whole tends to be less narrow than in *moschata*. Naef (*l.c.*, p. 723) points out that in this species, unlike any Octopod, the gill-retractors are fused in the middle-line.

*Alimentary canal.*—The mandibles are both stronger on the whole than those of *moschata*, the beak being better formed and larger. The dorsal mandible is better chitinized than in *moschata*. The radula has been figured by Jatta (*l.c.*, Pl. 28), Gravely (1909, Pl. 1) and Isgrove (*l.c.*, Pl. IV). My preparations differ somewhat from those figured by Jatta and Isgrove. On the whole they tend to be more like those of the latter, though Isgrove's figure is not very good. The rhachidian has an asymmetrical seriation. The admedian has a submedian cusp and marked

inner projection. The second lateral has a heel. The thick and heavy third laterals and marginals are very characteristic and with the admedians present a marked difference from those of *moschata*. The salivary glands, crop, stomach, coecum, intestine and ink-sac are all described and figured by Isgrove and do not differ significantly from those of *E. moschata*.

*Reproductive organs*. A. *Male organs*.—The hectocotylized arm is 69–76% of the longest normal arms. The hectocotylized part consists of ligula only, there being apparently no trace of a calamus (such as is (?) found in *E. moschata* occasionally). It is very short, 3·7–2·7% of the arm. The extremities of the rest of the arms are modified as in *E. moschata*; but in this case there is a single row of modified suckers. These are antero-posteriorly compressed and drawn out laterally into cirrus-like prolongations. The cavity of each sucker is very much reduced. Naef (*l.c.*, p. 724) speaks as though the male had specially enlarged suckers on the unmodified arms, whereas in the two males which I have seen the suckers are no larger than those of the female.

*Internal organs*.—Marchand (*l.c.*, fig. 33) figures a system quite definitely more like that of *Octopus* than that of *E. moschata*. Though Needham's organ runs direct into the penis there is a small penial diverticle (absent in *moschata*). Needham's organ is longer and more slender. The accessory gland is longer. The appendix penis is very well developed.

B. *Female organs*.—These have been described and figured by Isgrove (*l.c.*, Pl. V, fig. 39). As in *E. moschata* the vagina is narrow and the oviduct longer than in the Octopodinae.

*Habits, etc.*—In the Gulf of Naples this species is found on muddy and other bottoms (Lo Bianco, *l.c.*). Vérany (*l.c.*) and Jatta (*l.c.*) only allude to muddy habitats (cf. Joubin, 1920). Vérany's remarks suggest definitely that this species and *moschata* live together in shallow coastal water and that *cirrosa* alone is found at greater depths and farther from the coast. Several authors have commented on the rarity of the males. Pelseneer (1906) has laid it down that "the majority of Cephalopoda are hyperpolygynous," and Isgrove (*l.c.*, p. 472) states that at Plymouth (?) the females of *E. cirrosa* are fifty times as plentiful as the males. How far this disproportion is due in the case of *cirrosa* to the habits of the male is uncertain. The male, as Naef suggests (1912, p. 750), may keep in deep water and only the female come into shallow water for breeding. It is interesting to note that Isgrove (*l.c.*, p. 471) suggests that it lives in small groups of 2–6. Like other members of the group it seems to feed largely on crabs. Isgrove says (*l.c.*, p. 475) that only crab remains are found in the gut. *Cancer pagurus*, *Portunus depurator* and *Carcinus maenas*, as well as the Norway lobster and prawns and shrimps, are mentioned as food. It frequents lobster pots and no doubt feeds off *Homarus*. Nordgard (1923, p. 7) describes one eating a dead *Gadus* and previously syringing the latter with its siphon. As Isgrove (*l.c.*) suggests that it eats the mackerel used for bait it may be a carrion-eater. Joubin (in Isgrove, *l.c.*, p. 560 (? where)) states that it will eat its own eggs if disturbed. The only known enemies of the adult are the ling and angler (Isgrove, *l.c.*, p. 477); the same writer (p. 599) states that the eggs are attacked by crabs at least in an aquarium. The movements and general behaviour are described by Isgrove (p. 472). We may note (1) that the web is apparently not used in swimming (cf. Verrill), (2) the habit of getting

inside hollow vessels (cf. Part I, p. 22) and (3) of mound- or lair-building. Its health is very easily affected by captivity, and Isgrove (*l.c.*, p. 475) makes the very interesting observation that after a time it seems to lose the power of discharging its ink. Its delicate health in captivity may be partly due to a mild auto-intoxication due to the retention of the ink.

According to Lo Bianco, a few young individuals (40 mm. long) are found in the Gulf of Naples in April, and that much larger ones (120 mm.) are common in October. No other facts are known concerning the reproduction of the Southern form. Isgrove (*l.c.*, p. 559) found females depositing eggs in aquarium-tanks at Plymouth in July. From her observations it would seem that each female deposits about 30 separate clusters each consisting of 25–30 eggs. The clusters are not like those of *Octopus vulgaris*, as they seemed to be formed of sets of 4–6 eggs, the horny stalks of which are twisted together to form the main axis of the cluster (those of *E. moschata* are grouped in sets of 2–4, Naef, 1928, p. 278). The eggs are oval and measure up to 19 × 6·5 mm. (Isgrove) and are thus larger than those of *E. moschata*. The process of deposition is described by Gravely (1909, p. 1) and is of considerable interest. Apparently the proximal suckers and (?) the bases of the arms form a temporary ovipository chamber into which the eggs are placed by the funnel. From this they are ejected and fastened down by the small adoral suckers themselves. It is not known if the female incubates the eggs.

*Teratology.*—Appellöf (1893*a*, p. 1) gave an account of double hectocotylization, Parona (1900) has described a specimen of this species with a bifurcated arm and Girard (1890) one with seven arms.

*Remarks.*—The differences between this species and *E. moschata* are discussed on p. 260. Lamarck's first description does not distinguish the two species very clearly. His second, which recognizes the absence of the musk-like smell, the finely shagreened skin and certain colour-features, is quite clear on this point. The name of this species has been subject to more change than that of its ally *E. moschata*. "*E. aldrovandi*" has been used frequently and "*E. genei*" quite often. The specific name *aldrovandi* seems to go back to de Montfort's "poulpe d'Aldrovande." This is certainly an *Eledone*, but its specific identity is not clear. The name next appears as Rafinesque's *Ozoena aldrovandi* (1814), which is a *nomen nudum*. In 1820 Ranzani discussed *Octopus Aldrovandi*; he declared that de Montfort's species was "incerta e mal fondata" and that "non e certamente di quelli ad una sola fila di ventose, e non appartiene al genere *Eledone*." The identity of Rafinesque's *Ozoena aldrovandi* is not discussed. Orbigny (1826, p. 146) reaffirms Ranzani's criticisms, but he does not attempt to decide what Rafinesque's *O. aldrovandi* was. De Blainville mentions *O. aldrovandi*, but only repeats Ranzani's views. In 1830 delle Chiaje identified *O. aldrovandi* (the *aldrovandi* of Montfort and Rafinesque) with Sangiovanni's *O. leucoderma*, and said it was very like (? identical with) *O. cirrhosus* of Lamarck. His description is very slight, but he says (*l.c.*, p. 57) it is like *moschatus*, except that the smell of musk and the bluish line on the web are absent and the colour is less dark. Except for the second character which Naef, who has examined many living forms, ignores (1912, p. 749), the characters cited point definitely to *cirrhosus*. Vérany (1851) adopts the same differentia. By this time the identity of "*aldrovandi*," as distinct from *moschata*, had

become recognized, and there is little doubt that the species thus designated is the same as *cirrosus*. "*E. genei*," which was proposed by Vérany in 1837, was subsequently (*id.* 1851, p. 15) held by its author to be a variety of *aldrovandi* (= *cirrosus*). It appears to be a young *cirrosa*; but actually the sculpture is not mentioned. Grant's *ventricosus* and Sangiovanni's *leucoderma* are plainly synonymous with Lamarck's species. Rochebrune's imperfectly described *E. halliana* from Cherbourg is probably identical as well. I could not find the type of this species in the Musée d'Histoire Naturelle, Paris. The difference between *E. cirrosa* and *moschata* is dealt with on p. 260. Lamarck's original description remains valid, though I do not understand the statement "le bord du manteau est libre et détaché tout autour." This freedom of head and mantle is shown in his fig. 2 B, Pl. 1. I think the specimen must have been damaged. I do not know if one can identify Risso's *E. ambrosiaca* and *aldrovandi* (1854). To judge by the colour, the reddish or light brown *ambrosiaca* should be a form of *cirrosa*, the duller *aldrovandi* might be a form of *moschata*. He says, however, of *aldrovandi* that the ventral surface is "d'un blanc cendré," which is characteristic of *cirrosa*. Rochebrune's *Hoylea* (originally) *Hallia*, the type of which I have seen, is based on an example of *cirrosa* with wide peripheral ridge.

*Eledona albus* [sic] and *grisea* (Sardinia) of Arbanasich (1895, pp. 265, 266) may be referred to either of the two preceding species. Willemoes-Suhm (1876, p. 578) records an *Eledone* from 350 fms. off the coast of Brazil. No station-number was given and it is not to be traced among those described by Hoyle (1886).

### **Pareledone,** new genus.

The suckers are uniserial and the eggs are large. The hectocotylus is normal with well-developed ligula and calamus. Found in the Southern hemisphere only.

*Type of the genus.—Pareledone charcoti* (Joubin).

In 1918 Joubin separated the Mediterranean and N.E. Atlantic *E. moschata* and *cirrosa* from *E. verrucosa*, *challengeri*, *media*, *charcoti* and *turqueti*, the five last-named forms being placed in a genus *Graneledone*. As will be seen (p. 52), *charcoti* and *turqueti* differ very markedly from the three others placed in the same genus, and I have no option, but to separate them and place them together with certain other forms in a new genus, *Graneledone* being retained for *verrucosa* and *challengeri*.

#### **Pareledone charcoti** (Joubin).

*Eledone Charcoti*, Joubin (1905, p. 22, Pl. III, figs. 1–2).
„ „ *id.* (1906, p. 2, Pl. 1, figs. 1–2).
*Moschites charcoti*, Hoyle (1912, p. 279, text-figs. 6–7).
*Eledone Charcoti*, Joubin (1914, p. 35, figs. 1–2).
*Moschites charcoti*, Massy (1916, p. 151, text-figs. 12–21).
? *Moschites aurorae*, Berry (1917, p. 20, Pl. XII, fig. 9; Pl. XIII, figs. 10–12; text-figs. 14–20), see also postscript (1918).
*Eledone charcoti*, Odhner (1923, p. 6).
*Graneledone Charcoti*, Joubin (1924, p. 38).
„ *charcoti*, Robson (1930*b*, p. 388).

*Type.*—In M.H.N., Paris. (Holotype.)

*Specimens seen.*—(*a*) In Brit. Mus.

One (♀) from off Rio de Janeiro ("Terra Nova," 1919.12.30.17); one (♀) from off Oates Land (*ead.* 1919.12.30.18); three (♀) from the Ross Sea (*ead.* 1919.12.30.2–4); nine (4 ♂, 2 ♀, 3 juv.) from McMurdo Sound (*ead.* 1919.12.30.5 and 29–39); one (♂) from Butter Point, McMurdo Sound (*ead.* 1919.12.30.1).

(*b*) Coll. R.R.S. "Discovery."

Thirteen (5 ♂ 8 ♀) from South Georgia and vicinity.

(*c*) In M.H.N., Paris.

One (♀) from Wandel Island (type), two (? ♀) from Admiralty Bay, King George Island.

*Distribution.*—(*a*) Booth-Wandel Island (shore); Admiralty Bay, King George Island (S. Shetlands) (229 fms., mud and pebbles; + ·3°) (Joubin); Scotia Bay (S. Orkneys) (9–10 fms. 28°) (Hoyle); Oates Land, 69° 43′ S., 163° 24′ E. (179–200 fms.), Ross Sea, 74° 25′ S., 179° 3′ E. (157 fms., with bottom fauna), McMurdo Sound, 77° 13′ S., 164° 18′ E. (207 fms., bottom fauna, mud), Butter Point, McMurdo Sound (80 fms., bottom fauna) (Massy, 1916); off Queen Mary Land, 66° 8′ S., 94° 17′ E. (120–325 fms., small granite rocks) (Berry, as "*aurorae*"); South Georgia, various localities (114–6 fms., mud, algae, stones, etc.) (Odhner); South Georgia (0–142 fms.) (Robson). (*b*) South America. Off Rio de Janeiro (40 fms., bottom fauna, sand) (Massy).

*Description.*—The following description is based on all the available data. Important deviations from the original description are duly noted. The body is plump and saccular, its length usually (but not always) exceeded by its width. The head is definitely narrower than the body, and the eyes though fairly prominent are of moderate size. The arms tend to be subequal, though occasionally they differ fairly markedly in length. They are relatively short, having a range of 72–60% of the total length. The suckers tend to be small and to be little differentiated as between the sexes, though they are a little wider in the male. Their index of diameter ranges from 12 to 4·6, and they are normal in structure. The web varies somewhat in depth. Some forms with deep web (41–42) have been taken; but usually it is below 30% of the longest arm. On the whole it tends to have the formula A = B = C = D.E, but it is occasionally bilateral and E is sometimes as deep as A or even deeper. The sculpture is very variable. A description of the variation in the "Discovery" specimens is given by Robson (1930*b*). Expressed concisely the variation includes the following:—(1) closely opposed tubercles usually roundish, sometimes (?) branched (the type specimen); (2) a more granular type of sculpture, the tubercles being smaller and more widely spaced (Joubin, 1914, fig. 1). Between these two types there is every gradation. Thus there are forms with close, small warts and others with more widely-spaced, larger ones. Sometimes the warts are evanescent. Lastly, the distribution of the warts varies very much. In some they occur all over the dorsal surfaces and on the inner face of the web; in some they are limited to the anterior part of the mantle, head and web and are not found on the inner face of the latter. Ocular cirri may or may not be found. The funnel is wide and fairly prominent. The funnel-organ is V V-shaped; the lower part of each V is very thick, the

apices more narrow. In *aurorae* (Berry, *l.c.*, fig. 14) the organ is thinner and the limbs less coarse. The colour was not described by Joubin. In relatively fresh " Discovery " specimens it varies from a brownish-purple to light grey or fawn and is lightly reticulated with a darker colour. Berry's *aurorae* was " a dark slaty grey." The colour is paler below. The body usually exhibits a thin but clearly-seen dorso-lateral keel around the periphery.

*Structure of the tubercles.*—Joubin (1906, p. 6) made an investigation of the histology of the tubercles and concluded from the presence in them of muscular and lacunar tissue and a spiral (? muscular) axis that they are capable of considerable turgescence. However, they do not seem to differ in any marked way from the dermal papillae of other Octopods.

*Internal structure.*—The mandibles are normal. In Massy's figure (1916, p. 154, fig. 16) the rostrum of the upper mandible is relatively deep. The radula has been figured by Massy (*l.c.*, fig. 15). On the whole I can confirm her account of it. The admedians are narrow and rather taller than usual; the second laterals are simple with a rather narrow base and marginal cusps; the third laterals are straight and thick. The marginals are well developed. I only differ from Massy as to the median tooth, which I find to be taller than she indicates, its length considerably exceeding the width. Massy does not show the very deeply excavated inferior edge of the basal plate. These teeth have two ectocones aside. The posterior and anterior salivary glands are both well developed and the crop is normal and *Octopus*-like. The rest of the alimentary canal is normal. The ink-sac, as Massy says, is smaller than that of *E. cirrosa* in the three specimens I have examined. It is completely buried in the liver and is not visible from the exterior. There are 8–11 filaments in each demibranch. Massy (1916, p. 153) says the main features of the pallial respiratory organs are like those of *E. cirrosa*.

*Reproductive organs.* A. *Male.*—I agree with Massy in her general account. The spermatophores are very large (about 80 mm. long in males measuring 52 mm. in mantle-length). They tend to be of a simpler and less differentiated pattern than in *Octopus*. I find that there are usually two only in Needham's organ. There is a moderate appendix to the prostate and a large saccular penial diverticle. The penis itself is short and thick. *The hectocotylus.* The hectocotylized arm is usually not very much smaller than the others, and is about 89–79% of the longest arm. The hectocotylus is 11–4·6% of the arm. The ligula is broad and pointed. Its strongly thickened sides produce a deep copulatory groove which is faintly laminate. The calamus is acute but very short. The organ is a better developed and more robust version of that of *E. verrucosa*.

B. *Female.*—Massy (*l.c.*, p. 154) found a female of 35 mm. mantle-length with the ovary full of eggs 1·5 mm. long. On the other hand, I have found eggs with the following dimensions :—

| " Discovery " Stn. | Mantle-length. | Size of eggs (mm.). |
|---|---|---|
| 39 | 60 | 9 × 5 |
| ,, | 74 | 13 × 7 |
| ,, | 41 | 3·5 × 1·7 |

The oviducts are short and joined in the middle line. The spermathecae are of moderate size. The vaginae are very short and thick; their diameter is perhaps less than that of the spermathecae in Massy's figure. In one specimen I have examined it is, however, wider.

*Habits.*—This is a particularly widespread species ranging about five-eighths of the way round the Antarctic continent (S. Orkneys, S. Shetlands, Ross Sea, Oates Land, Queen Mary Land). It has a great tolerance of cold conditions (see below). Its distribution from Rio de Janeiro to the recesses of McMurdo Sound is a testimony to its eurythermic capacity. It penetrates into higher latitudes than any known Octopod except *B. arcticus*. On the other hand, its tolerance of low temperature must be far greater than that of *arcticus*. The latter only attains its present "farthest-north," because it avails itself of the warm Atlantic current which takes it as far north as N. Spitzbergen. In the colder water of Davis Straits it gets no farther north than 67° N., whereas *G. charcoti* reaches McMurdo Sound (77° S.). It seems to live on a variety of bottoms. Its vertical range is not extensive, the maximum depth attained being 420 m. (Joubin). From Massy's account of the stomach contents (*l.c.*, p. 155) it would seem that this species feeds on benthic forms of various groups and does not confine itself to Crustacea, and that it is probably a carrion eater.

*Remarks.*—There does not seem to be any reason for questioning Berry's tentative identification (1917, appendix [1918]) of his *aurorae* (Queen Mary Land) with Joubin's species. Similarly I concur in Massy's identification of a specimen from Rio de Janeiro. This is a very variable species (cf. Robson, 1930*b*, p. 389); but on the whole it is fairly easy to recognize.

### **Pareledone turqueti** (Joubin).

(Text-fig. 50.)

*Eledone Turqueti*, Joubin (1905, p. 29, Pl. III, figs. 3–6).
,, ,, *id.* (1906, p. 9, Pl. 1, figs. 3–6).
,, ,, *id.* (1914, p. 37, text-figs. 3–4).
*Moschites turqueti*, Massy (1916, p. 155, text-figs. 22–28).
,, ,, Berry (1917, pp. 13–14).
*Graneledone Turqueti*, Joubin (1924, p. 38).
,, *turqueti*, Robson (1930*b*, p. 390).

*Type.*—In M.H.N., Paris (one ♀). (Holotype.)

*Specimens seen.*—(*a*) in Brit. Mus.

Two (♂ ♀) from Cape Evans, McMurdo Sound ("Terra Nova," S. 355); one (♀) from Rio de Janeiro ("Terra Nova," S. 42).

(*b*) "Discovery" Collection.

Three adults (2 ♂ 1 ♀), two young from the Palmer Archipelago, Danco Land (Stn. 181); three young (♂ ♀ ?) from off S. Georgia (Stn. 158).

(*c*) In M.H.N., Paris.

One (♀) (the type); two (♀) from 2$^{me}$ Exp. antarctique Française.

*Distribution.*—Booth Wandel Island, Danco Land, in 13 fms., Admiralty Bay, King George Island (S. Shetlands), in 229 fms. (Joubin); Cape Evans, McMurdo Sound, 77° 46′ S., 166° 8′ E., in 300 fms., off Inaccessible Island, McMurdo Sound, in 222–241 fms. (Massy); Schollaert Channel, Palmer

Archipelago, in 183–87 fms., N. of S. Georgia, in 224–219 fms. (Robson); off Rio de Janeiro, in 40 fms. (Massy).

*Description.*—As will be seen from the following data the identity of the various specimens that have been assigned to this species is very questionable. It should be borne in mind (see below) that it is not certain that Joubin's second series are referable to *turqueti*. The type has a square body, its width and that across the eyes being equal to the length. The eyes are scarcely prominent and there is no postocular or preocular constriction. In the S. Shetlands form the eyes are far more prominent and the body is relatively much wider. The forms identified by Massy have been so much damaged that I cannot describe them. They seem to have been narrower and the head distinctly narrower than the body. The same is true of the " Discovery " specimens. The arms in all the series tend to be subequal. In the type there is a difference of 4 mm. between the longest and shortest arms. The length tends to be alike in the four series and to range from 64–72% of the total length. The suckers are small (probably a little larger in the male) and of normal structure. In his earlier account Joubin treated as of systematic importance the fact that on the dorsal arms the suckers are mostly arranged in two rows. In his later observations (1914, p. 37) he evidently found the normal arrangement in three out of his four specimens. I conclude that such idiosyncratic (perhaps artificial) tendency to the biserial arrangement has no real importance. The size of the web is unfortunately a matter on which Joubin's two versions differ very markedly. In his first description (1906, p. 11) he says it " occupe à peine une cinquième de la hauteur des bras." In the figures subsequently published (1914, figs. 3–4) it is plainly far longer. In figure 3 sector B is over half the length of the arms. In the " Terra Nova " specimens it is 38–28%, and in the " Discovery " *c.* 25% of the arms. The funnel is small, its organ VV-shaped and usually thin-limbed. The surface of the web, head and the sides of the arms in the type and the S. Shetland specimens are covered with sparse granulations. The " Terra Nova " specimens are not in good condition and I cannot speak of the sculpture. One of the " Discovery " specimens is quite smooth, the other has some patches of small pustules which may be of artificial origin. The colour is of a violet shade or of a more definite brownish-purple. The mantle-aperture is narrow (B or B–C). There are 10–11 filaments in each demibranch. The inner demibranch is little reduced. The mandibles are normal. The *radula* of the type was not described. That of a " Terra Nova " specimen was figured by Massy (*l.c.*, fig. 27). I have examined that of the male described by me under this name in the " Discovery " report. A very serious discrepancy offers itself between these two specimens. Massy's drawing of her specimen does not correspond very closely with the preparation made by her from the " Terra Nova " specimen from Stn. 355, as there are marked differences in the first lateral. Be that as it may, the " Discovery " specimen has a radula very unlike that of the " Terra Nova " example (text-fig. 50). The rest of the digestive system is normal and like that of *M. charcoti*. The ink-sac is deeply imbedded in the liver, but it is placed nearer the surface than in *charcoti* and a small portion of it is just visible.

*The reproductive organs.* A. *Male.*—The male organs of the single

large " Discovery " specimen are in a rather undeveloped condition, Needham's organ being very small. I could find no spermatophores. The penis seems to resemble that figured by Massy (fig. 22). It has a large diverticle. The hectocotylus is small (*c.* 7·7%) and may be undeveloped, in which case it might well grow into a form like that figured by Massy, although at present it is very distinct. The ligula is very short and broad and the calamus wide and scarcely folded-in at the sides. Massy figures an organ quite like that of *charcoti*.

B. *Female*.—Here again we find a marked difference between Massy's drawing (fig. 24) and the " Discovery " specimen. In the former there is practically no oviduct and the spermathecae and vaginae are large. In the " Discovery " specimens the system is delicate and slender; the

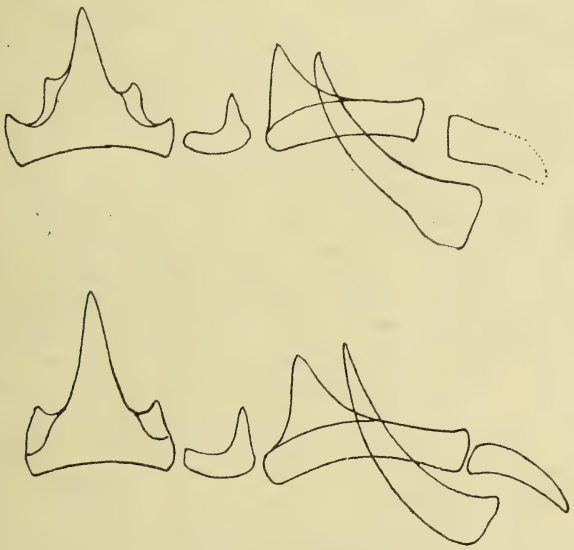


Fig. 50.—*Pareledone turqueti*. Radulae of " Discovery " (above) and " Terra Nova " specimens.

oviduct and vagina are of equal length and the spermathecae are small. In both the eggs are small, *e.g.* in the " Discovery " specimen, about 1·5 mm. long.

*Habits*.—This species has the same wide distribution as *P. charcoti*. Like the latter it penetrates into the recesses of McMurdo Sound. It ranges from 25–420 m. in depth. The stomach of one of the " Terra Nova " specimens contained " much digested animal remains and crustacean ( ?) ova."

*Remarks*.—The identity of the various specimens that have been assigned to this species is very much open to question. It will have been already seen that Joubin assigned to his species some specimens differing from the type in certain material respects, and there are marked differences between Massy's specimens and my " Discovery " ones. Until, however, we have a long series of adult specimens for comparison it is useless to speculate on the identity of these forms, and rather than complicate the situation by the description of more species on insufficient material, I

have here confined myself to setting forth the particular features of the various specimens and series that have received this name.

**Pareledone polymorpha** (Robson).

(Plate V, fig. 1.)

*Graneledone polymorpha*, Robson (1930*b*, p. 390, Pl. III, fig. 1).

*Type.*—In Brit. Mus. (Holotype.)

*Specimens seen.*—" Discovery " Expedition. Twenty-four specimens (including type) (15 ♀ 9 ♂) from South Georgia.

*Distribution.*—South Georgia (*passim*) in 149–8 fms.

*Description.*—This species occurs in two phases, the external features of which are described separately. (*a*) Form *oblonga* (Brit. Mus. 13iv, 10iv, 5i). The mantle is narrow and oblong (75–64), and the head is only a little narrower (69–61%). The arms are subequal and short (72–65%). The suckers are small (7–8%), and the web is deep (40–35%). It is distinctly and regularly bilateral, but the various sectors do not differ very much in depth, A and E being about equal. The colour tends to be a very light purplish-brown, in one specimen becoming a distinct mauve-fawn. The circumpallial ridge is little developed. The sculpture consists of rather widely spaced small granules. In 5 (i) these are rather wart-like. The hectocotyli of 5 (i) and 10 (iv) are long (15–13·9%) and very much alike. The calamus is acute and erect, the ligula shallower than in *charcoti* and crossed by a number of well-marked laminae. (*b*) Form *affinis*. (Brit. Mus. 12, 1, 9, 11, 14). The mantle is ovoid and wide (104–70). The head is narrower than the body and usually the eyes are prominent. The web as in (*a*) tends to be bilateral; but there is even less difference in the width of the various sectors than in (*a*). The maximum depth is less (30–27%). The colour is usually a greyish-purple tending to a colder slaty hue. There is usually a strong circumpallial ridge. This form is otherwise like form *oblonga* in its external features. The sculpture also resembles that of form *oblonga*. The hectocotylus is 17–9% of the arm. It resembles that of *oblonga*, though the copulatory groove is narrower. The mantle-aperture in both forms is rather on the narrow side (B). The funnel is short. The funnel-organ is **W**-shaped. There are 10–17 filaments in each demibranch; the inner demibranch shows a certain amount of reduction. The mandibles are normal. *The radula.* The rhachidian has a long stout mesocone, the height of which exceeds that of the base. On some teeth there are traces of ectocones in this series; but they are in the mass unicuspid. The admedian is small, with an oblong base and a low blunt entocone. The second lateral has a rather narrow and shallow base with a low, heavy, subterminal cusp. The third laterals are small, much curved with characteristic thick tips and wide bases. The ink-sac is completely buried from sight in the tissues of the liver in both forms. In all specimens examined it is rather small. The crop is tolerably well developed. The posterior salivary glands are very large. The stomach contained very finely comminuted Crustacean remains with remnants of bottom débris, Polychaete bristles and fish-scales.

*Reproductive organs.* A. *Male.*—Needham's organ contains 2–3 (? more) large spermatophores measuring 50–55 mm. These have large

heads, but are smaller and less bulky than in *charcoti*. The accessory gland has a well-marked appendix and the penis a large diverticle. The hectocotylus is large and well formed. It is 17–9% of the arm in length. The ligula has thick sides and a deep and narrow copulatory groove crossed by 7–8 well-marked laminae. The calamus is short and subbasal; its extremity does not reach half-way from the last sucker to the end of the ligula.

B. *Female.*—The eggs (in two large specimens) measure about 8·5–9 × 3·5 mm. The oviducts are extremely short, the spermathecae being more or less in contact with the ovary. The spermathecae are large, the vaginae stout and rather short, tapering somewhat towards the extremities.

*Remarks.*—Of all the related forms this species has the closest affinity with *charcoti* and *harrissoni*. I must, however, maintain my original view that it is quite distinct from both those species. From *harrissoni* it differs in (1) the form of the funnel-organ, (2) sundry details in the radula, especially in the form of the admedian and laterals, (3) the form of the eyes, head and body and the greater depth of sector A of the web in *polymorpha* (16–22% in *harrissoni* and 22–28% in *Polymorpha*). From *charcoti* I consider it sufficiently well distinguished by (1) the form of the funnel-organ and radula (especially in several details of the latter), (2) hectocotylus and (3) the narrower and more ovoid body. The regular presence in it of a well-developed circumpallial ridge may be also considered a difference of some value, though I am not yet satisfied as to its importance. However, in the array obtained by the "Discovery" there are several examples of ambiguous status. The sculpture in particular is not confined to a single uniform type.

### **Pareledone harrissoni** (Berry).

*Moschites harrissoni*, Berry (1917, p. 24, text-figs. 21–25; Pl. XIII, fig. 13; Pl. XIV, figs. 14–16).

*Type.*—In Australian Museum, Sydney. (Holotype.)

*Distribution.*—Shackleton ice-shelf, Queen Mary Land, Antarctica in 270–358 fms.

*Description.*—The species is only known from female specimens. The body is rounded and plump and broader than long. The head is small and narrower than the body. The eyes are large and conspicuous. The arms are stout and very short (69–65%). The dorsal arms tend regularly to be shorter than the rest, which are subequal. The suckers are regularly uniserial. From Berry's figure (p. 24) I calculate that the diameter in the type is 8·8% of the mantle-length, so that they should be regarded as small. The web is bilateral and usually a little deeper ventrally than dorsally. It seems to be about 25% of the arm-length. The surface is said to be smooth; but there are "a number of low conical papillae scattered irregularly over the dorsum and sides, around the eye-openings and on the bases of the four dorsal arms." There is a distinct subperipheral ridge around the body. The colour is a dull clouded slaty grey, paler ventrally and on the inner surface of the arms. The mantle-aperture is wide (? C), the funnel stout and conical extending over half the distance to the margin of the web. The funnel-organ is VV-shaped, with

fairly broad limbs. The mandibles are normal. The radula is well developed. The median teeth are tall, their length exceeding the base. They have regularly a single ectocone on each side, " intermediate cusps being present on certain teeth as well " ( ? symmetrical seriation). The admedians are small and have blunt points. The second laterals have a long rectangular base, a strong mesocone and practically no inner heel. The third laterals are long and slightly curved with moderate bases.

*Remarks.*—Berry (*l.c.*, p. 27) compares the radula and funnel-organ with that of his *aurorae* (= *charcoti*). The two species are, however, otherwise pretty clearly distinguished. The same is true of the relation between *harrissoni* and *polymorpha* (p. 277). At present these three forms seem to be quite distinct, though there tends to be a good deal in common between them. It is possible that a more plentiful supply of specimens might reduce the observed differences.

**Pareledone adelieana** (Berry).

*Moschites adelieana*, Berry (1917, p. 17, Pl. XI, fig. 5; Pl. XII, figs. 6–8; text-figs. 10–13).

*Type.*—In the Australian Museum, Sydney. (Holotype.)

*Distribution.*—66° 55′ S., 145° 21′ E., off the Mertz Glacier Tongue, Adelie Land, Antarctica, in 288–300 fms., in ooze.

*Description.*—The species is mainly known from a single female specimen. The body is rounded and very short and broad. The head is very large, its size being due to " the immense, swollen eyes, which nearly meet in the median line above." The arms are very short (69%), with the extremities " little attenuate." The order is uncertain, but it may be 4.3.2.1., with very little difference between the arms. The suckers (as calculated from Berry's figure, p. 18) are about 8% of the mantle-length and are uniserial throughout. The web is bilateral, though there seems to be but little difference between the various sectors. It is scarcely 25% of the arm-length. The surface is entirely smooth. The colour (in alcohol) is " a dull-coloured slaty grey, only slightly paler below, though quite pale under and around the funnel." There is a subperipheral pale line, but no ridge. The pallial-aperture is wide (C), the funnel cylindrical and reaching a little less than two-thirds of the distance to the edge of the web. The funnel-organ is W-shaped, its limbs being pointed at the extremities. The mandibles are thin and fragile. The superior mandible seems weakly developed and to be little differentiated on the cutting surface. The radula is well developed. The median teeth have sharp and tapering points, and the main cusps are slightly shorter than the width of the base. Berry could distinguish no lateral cusps. The admedians are small and triangular. The second laterals are provided with large cusps and ( ?) an inner heel, which does not, however, bear a cusp. The base is not clearly seen in Berry's drawing, but it seems to be short. The third laterals are long, curved and apparently provided with fairly wide basal plates.

*Remarks.*—Berry (*l.c.*, p. 20) compares this species with *turqueti*, and there seems to be a general resemblance between the two forms. I have already, however, shown that the characters of *turqueti* are by no means exactly known. Unfortunately Joubin's description was based on a

single young specimen and contained no description of the radula and funnel-organ. Massy and I have identified and described certain forms as referable to *turqueti* ; but it will be seen (p. 275) that these identifications can only be treated as provisional. It is therefore impossible at the present moment to criticize the status of Berry's species.

**Pareledone nigra** (Hoyle).

*Moschites nigra*, Hoyle (1910*a*, p. 262, text-fig. 2).
„ „ Berry (1917, p. 13, ref. only).

*Type.*—In Z.M. Berlin. (Holotype.)

*Distribution.*—Luderitzbucht, Angra Pequeña, S.W. Africa, among rocks in shallow water (Hoyle, *l.c.*, p. 261). Only known from the type-locality.

*Description.*—The body is " flattened ovate, broader behind than in front." The head is rather narrow and the eyes " not very prominent." The arms are subequal and, for an *Eledone*, rather long, viz. 78% of the total length. The suckers are regularly uniserial, but towards the base of the arm, where the largest suckers occur, there is a tendency to the alternating arrangement, though the suckers do not form two definite rows. The largest suckers attain a considerable diameter for an *Eledone* (15%). The web is rather shallow (25) and E is less well developed than A. The mantle-aperture is wide (B–C). The funnel is slender and conical and reaches half-way to the edge of the web.

*The radula.*—The rhachidian has usually two cusps aside, there being an asymmetrical seriation. The admedians seem to be rather like those of the " Discovery " *turqueti*, *i.e.* they have a rather long cusp and wide base. The second lateral has a very marked heel, and the third lateral is much curved and has a wide base. The radula as figured by Hoyle (*l.c.*, p. 263) is distinctly *Octopus*-like, and can hardly be distinguished from that of many species of the latter genus.

The surface is " practically smooth," though there are vague traces of a " shagreen-like " pattern. The *colour* is " a very deep brown, almost black."

*Remarks.*—The species is known from a single male and six females obtained in shallow water. The hectocotylus of the male is undeveloped. It seems to be an interesting form, as from the radula one would rank it as the least modified of the *Eledone*-like forms.

**Pareledone antarctica** (Thiele). (? = **P. harrissoni,** Berry).

*Moschites antarcticus*, Thiele (1920, p. 434, Pl. LII, figs. 1, 2).

*Type.*—In Z.M. Berlin. (Syntypes.)

*Distribution.*—" Gauss " Station, Gaussberg, Kaiser Wilhelm II Land (*c.* 89° 20′ E., 66° 47′ S.), depth unknown. Only known from the type-locality.

*Description.*—In the following description the various proportions given are calculated approximately from Thiele's measurements as follows :—

1. ♂. " An der Seiten 82 mm. long." I take this to mean that the length measured is the side of the mantle, *i.e.* that it does not include the

distance from the mantle-edge (ventral) to the centre of the eye. In order to obtain my apex-eye measurement I have made Thiele's 82 mm. up to 95. The indices here given are subject to this qualification.

2. ♀. "Körper ist bis zum Vorderende des Mantels 10 cm. long." I have used 115 mm. as the mantle-length.

3. ♀. "Länge des Mantels etwa 93 mm." I assume that the second female was measured in the same way as the first, and have accordingly used 107 mm. as the total mantle-length.

The body (in the male) is round-oval in shape, with its maximum width half-way from the apex. Its width varies from 52% to 63% of the length. The head is narrower. The eyes are only moderately prominent. The ventral arms are usually longer than the dorsal; the maximum arm-length is 65–62% of the total length. The suckers (of the male) are described as having "mässige Grösse," but the measurement given yields the low index of 5·2–6·3%. In the male they have a zigzag arrangement, and according to Thiele and Chun (MS.) are arranged far more like those of an *Octopus*. In the females they are "im ganzen einreihig doch fast an allen Armen stellenweise mehr oder weniger deutlich zickzackförmig geordnet." (Thiele, *l.c.*, p. 435.) The web in the male is "3 cm. *breite*" (*i.e.* 16% of the arms), in the larger female almost 6 cm. (32%). In the latter E is plainly deeper than A. The hectocotylized arm is 1 cm. shorter than its fellow. The length of this is not given. I provisionally calculate it as 175 and the hectocotylized arm as 165. On this assumption the end-organ would be about 4·2% of the arm. The end-organ is vaguely like that of *turqueti* and *charcoti* in that the calamus extends about half the length of the whole organ, and the sides of the ligula thick marked and deeply scored by the laminae. In *antarcticus*, however, the copulatory groove is smaller and the calamus reaches over half the length of the whole organ, whereas in *charcoti* it attains under half the length. In the male the skin is "bis auf die wahrscheinlich infolge der Konservierung entstandenen Runzeln glatt." One of the females exhibits on the dorsal surface a number of small warts; the other scarcely shows any trace of these. The male is of an indefinite grey-yellow.

*Remarks.*—Thiele's description is rather meagre and it is not accompanied by a figure of the whole animal. It is distinguished from *charcoti* by (*a*) the absence of characteristic sculpture, (*b*) the shape (?) of the web and (*c*) the length of the hectocotylus; from *turqueti* in (*a*) body shape, (*b*) size and form of the hectocotylus and (*c*) form (?) of the web (?); from *polymorpha* in (*a*) form and size of the hectocotylus and (*b*) size of the suckers. It is possibly synonymus with *harrissoni* (Berry, 1917, p. 24). It agrees with that form in having the fourth arm regularly longer than the first and of very moderate length, in the fact that in the web E is greater than A (?) and in the surface tissues. The body of *harrissoni* is much wider, the eyes are much larger and more prominent. Unfortunately there is not much common ground in the two descriptions. It must be noted that *E. harrissoni* was taken from off Queen Mary Land (*i.e.* not far from the Gaussberg). This species requires a fuller description and may eventually prove to be synonymous with one of the previously described forms.

**Pareledone** sp.

" *Moschites brevis* Hoyle," Massy (1916, p. 158, text-figs. 29-32).

*Specimen seen.*—One (♂) from Rio de Janeiro.

*Distribution.*—Off Rio de Janeiro (22° 56′ S., 41° 34′ W.), in 40 fms., with bottom fauna on sand.

*Description.*—The body is saccular and round, the head narrower than the body. The arms are short (? 64%) and probably subequal. The suckers are rather large and prominent. The web is subequal in all the sectors save the last, which is a little shorter than the rest, and very deep (45%). The whole surface, except the ventral part of the web, is covered with low pustules. In addition, there are a number of low warts on the dorsal surface and a large cirrus over each eye. The dorsal surface is covered with a dark purple reticulation very like that of *Octopus rugosus*. There is a distinct subperipheral keel. The mantle-aperture is wide (B–C). The funnel is rather tubular. Its organ is VV-shaped, the bases rounded, the tips of the limbs pointed (Massy, *l.c.*, text-fig. 30). The *radula* has a rhachidian with symmetrical seriation and two cusps a side. The admedian has a low ectocone and traces of an entocone. The second lateral has a large heel and long base. The third laterals are heavy and sickle-like. The marginal plates are well developed. The radula on the whole is indistinguishable from that of many species of *Octopus*.

The ink-sac is present and, though sunk in the surface of the liver, is plainly visible. The hectocotylus is minute and its parts undeveloped. The internal genitalia are likewise very undeveloped.

*Remarks.*—This specimen is obviously immature. It is most emphatically unlike Hoyle's *E. brevis* now placed in *Thaumeledone*, from which it differs in bodily shape, sculpture, presence of an ink-sac and well-developed radula. Although the funnel-organ is more slender and the two forms differ quite markedly in the radula, the general facies and sculpture remind me of certain forms of *P. charcoti*.

**Eledonenta** (?), de Rochebrune, 1884.

*Type of the genus.—Eledonenta filholiana*, de Rochebrune.

This genus was proposed by de Rochebrune for a species (*E. filholiana*) from Fiji and one from the Red Sea (*E. microsicya*). The definition of the genus gives us very little clue to its identity :—" corps longuement ovoïde, étroit, plus ou moins rugueux; tête petite, quadrangulaire, yeux assez larges, peu saillants, surmontés d'un cirrhe fortement conique, obtus; bras excessivement longs, aplatis, à cupules grosses, cylindriques, disposées sur un seul rang mais irrégulièrement distribuées et donnant aux bras l'aspect d'un intestin mameloné [sic]; membrane de l'ombrelle peu developpée, mince, comme flottante, se prolongeant jusqu'au premier tiers des bras en une crête assez élevée; tube locomoteur long et cylindrique."

I have examined the types and other specimens of *E. microsicya* and *filholiana* in Paris and have formed the conclusion that *microsicya* is in all probability a specimen of *Eledone*, though the only specimens being female it is impossible to make certain to what species we should refer it. The only clue is the smooth skin which suggests that they may be referable

to *E. moschata*. *E. filholiana* is fortunately represented by a male. Its hectocotylus is not like that of *Eledone*. It is very narrow and pointed and has a small basal calamus. It is not unlike that of *Octopus dofleini* (see Part I, p. 130). I could find no indication other than the arrangement of the suckers that this is not a normal *Octopus* with widely alternating suckers. This genus, which was distinguished on quite trivial grounds, should be abandoned, *microsicya* being placed in *Eledone* and *filholiana* in *Octopus*.

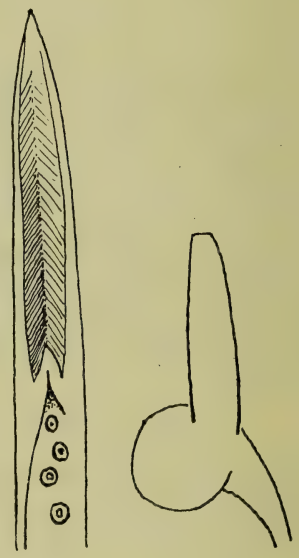
**Eledonenta (? Octopus) filholiana,** de Rochebrune.

(Text-figs. 51–52.)

*Eledonenta Filholiana*, de Rochbrune (1884, p. 157).

*Type.*—In M.H.N., Paris. (Holotype.)
*Specimen seen.*—The type.
*Distribution.*—Fiji Islands.
*Description.*—

Fig. 51.—"*Eledonenta*" *filholiana*. Suckers (diagrammatic). (M.H.N., Paris.)



*a* *b*

Fig. 52.—"*Eledonenta*" *filholiana*. (*a*) Hectocotylus; (*b*) Penis. (M.H.N., Paris.)

"*Eledonenta filholiana*.

"Corps ovoïde, allongé, finement rugueux; tête petite, quadrangulaire yeux assez grands, un peu saillants, surmontés d'un cirrhe large conique; bras presque égaux, très longs, grêles, aplatis, à cupules larges noueuses, irrégulièrement distribuées sur une seule rangée; membrane de l'ombrelle peu développée, transparente et comme flottante. Animal de couleur rouge vineux pâle, piqueté de très petits points bruns et marbré de larges taches violettes.

Long. corp . . . . . 0,100.
Lat. „ . . . . . 0,047.
Long. med. brach. . . . . 0,410.

Hab.—Îles Fidji (M. Filhol). Type, Mus. Paris."

I append the measurements (mm.) of the specimen in its present condition. Mantle-length, 97; mantle-width, 47; head-width, 23. Arms, R. 448, 448, 226, 320, L. 446, 395, 346, 346. Web, 70, 70, 63, 65, 46. Hectocotylus, 13. There is no trace of modification of the other arms. The penis is retort-shaped. The ink-sac is normal.

**Eledonenta (? Eledone) microsicya,** de Rochebrune.

*Eledonenta microsicya*, de Rochebrune (*l.c.*, p. 158).
*Moschites* (*Eledone*) *sp.*, Wülker (1920, p. 52).

*Type.*—In M.H.N., Paris. (Holotype.)
*Specimens seen.*—The type and (?) paratype.
*Distribution.*—Red Sea.
*Description.*—

" *Eledonenta microsicya.*"

" Corps ovoïde, arrondi en arrière, finement réticulé sur la face supérieure; tête petite, arrondie; yeux également petits, surmontés d'un cirrhe conique et élevé; bras grêles, presque égaux, subarrondis, longs et très effilés à la pointe, à cupules d'une extrême petitesse, disposées sur un seul rang dans toute la longueur des bras; membrane de l'ombrelle large, mince, à peine transparente; animal d'un jaune sale, finement piqueté de très petits points noirs et orné de larges taches bleuâtres.

" Cette espèce, assez voisine de la précédente, en diffère cependant par les réticulations de la face supérieure du corps, par la petitesse des cupules, l'aspect des bras beaucoup moins moniliformes, par la disposition de l'ombrelle et une coloration tout à fait différente.

Long. corp . . . . . 0,060.
Lat. „ . . . . . 0,025.
Long. med. brach. . . . . 0,109.

Hab.—Mer Rouge (Clos-Bay). Type, Mus. Paris."

The following are the measurements (mm.) of the type. Mantle-length, 51; mantle-width, 32; head-width, 19. Arms, subequal, *c.* 140. Web, 50, 48, 45, 40, 28. The skin is smooth. The suckers were probably uniserial.

**Velodona,** Chun, 1915.

" Eledonid " Octopodines in which the ventral membranes of the arms are markedly expanded and the funnel-organ consists of two moieties each shaped like an exceedingly thick V. The relation between penis and diverticle is like that of *Eledone cirrosa*. There is no appendix of the accessory gland, and Needham's organ is very small (?). The ink-sac is degenerate (?).

*Type of the genus.—Velodona togata*, Chun.

The status of this genus is rather difficult to determine. The enlargement of the ventral arm-membranes and the peculiar funnel-organ are

singular and characteristic features. The male genitalia (concerning which there is some ambiguity) and suckers are *Eledone*-like. The hectocotylus of the type is not unlike that of some sub-Antarctic *Pareledone*. The radula might be that of a *Bathypolypus* or of *Graneledone*. The peculiar sigmoid bend of the hectocotylized arm described by Chun and evidently regarded by him as of diagnostic value seems to me to have been produced by contraction. It is not seen in the large male of subsp. *capensis*. On the whole, *Velodona* seems to me to be an Indian Ocean offshoot of the *Pareledone* stock.

**Velodona togata,** Chun.

*Velodona togata*, Chun (1915, p. 479, Pls. LXXV, LXXVI, text-figs. 47–50).

*Type*.—(?) In Z.M., Berlin. (Holotype.)

*Distribution*.—Station 249, "Valdivia," (?) just N. of Zanzibar, in 409 fms.

*Description*.—The body is described as "plump sackförmig gestaltet, hinten abgerundet und breiter als lang." Actually in the figure on Plate LXXVI the body looks narrower and more oblong. The head is wide, the eyes large and prominent "und deuten hierdurch auf den Aufenthalt in der Tiefe hin." The arms are in the order $1 > 4$, but their length is not given. The dorsal arms bear 102 suckers. I have estimated the diameter of the suckers from Plate LXXV as 6·6% of the mantle-length and therefore small. The length and form of the web is not given precisely and cannot be exactly inferred from the text or figures. Sector A seems to be (Plate LXXV) about 20% of the arms. Sector B is expanded on the ventral side of the first arm as the wide membrane characterizing the genus. The same broad membrane is found on the second and third arms decreasing in width successively towards the third. The last sector (E) seems shallower than A. The whole dorsal surface of head, mantle and the outer surface of the two pairs of dorsal arms is covered with fine multifid warts. There is a large cirrus over each eye and another at the root of each dorsal arm. The colour seems to have been a purplish-brown on head and dorsum, becoming much paler laterally and ventrally. The width of the pallial aperture is not indicated. The adhesive-organ is well developed and there is a strong siphonal ridge. The funnel is broad-based and rather short. The funnel-organ is said to consist of two broad "Lappen" which "in Verhältnis zu der Grösse des Trichters ein nicht gerade ansehnliche Entwickelung aufweisen." The gills are large (30 mm. long) and consist of 8 broad filaments a side. The hectocotylus is well developed. As the length of the arm is not given its length cannot be expressed in the usual way. Expressed as a percentage of the mantle-length it is about 12%. In *P. polymorpha*, a form with a rather large end-organ, the length of the latter expressed as a similar percentage is 25%, from which we might infer that the organ in *togata* is half the size of that of *polymorpha*. The rather narrow and pointed ligula has a deep and narrow groove crossed by 15 laminae. The calamus is basal and small. Chun notes that the third right arm, which is remarkably short to judge by the number of suckers (less than half those on first arm), is bent in an S shape. Whether this is natural or

merely due to an extra strong contraction of the membrane it is impossible to say.

*Remarks.*—The radula, internal genitalia and sundry other features are described under the variety *capensis*. It is a little unfortunate that Chun gave no measurements of the arms and web-sectors.

**Velodona togata,** subsp. **capensis,** Robson.

*Velodona togata*, Chun, var. a, Robson (1924, p. 206, fig. p. 207).
,, ,, var. *capensis*, Robson (1924*a*, p. 655, text-figs. 30–32).

*Type.*—In Brit. Mus. (Holotype.)

*Specimens seen.*—Four specimens from Natal Coast (" Pickle," Stns. 99, 162, 396).

*Distribution.*—Coast of Natal, in 220–250 fms.

*Description.*—The body and head have about the same proportions as in the type of the species (Chun's figure). The arms (length in type unknown) are 78–77% of the total length and are in the order 1.2.3.4. The first arm is markedly longer than the rest. The suckers are 7·5–5·2% of the mantle-length. The web is bilateral (CB = ADE) and, as in the type, E is definitely shallower than A. The ventral membrane of the arms has the following width :—

| | | |
|---|---|---|
| 1st | arm . . . . . | 38 mm. |
| 2nd | ,, . . . . . | 27 ,, |
| 3rd | ,, . . . . . | 14 ,, |
| 4th | ,, . . . . . | 9 ,, |

The sculpture resembles that of the type, though the warts are denser and more spinose on the average and there are more pallial cirri. The colour tends to be deeper than in Chun's specimen; but its general distribution is the same. In both males and females there is a peripheral ridge not described by Chun in his specimen. The funnel-organ seems to be as described for the type. Its members are remarkably thick, thicker indeed than in any species of *Eledone* (Robson, 1924*a*, text-fig. 30). The mandibles are normal and well developed (Robson, *l.c.*, text-fig. 31). The *radula* is simple. The rhachidian is unicuspid. The admedian has a rather high thick cusp. The second lateral has a heavy terminal cusp and a short base. The third lateral is remarkably thick and short. The anterior salivary glands are very small, almost minute, the posterior large and about six times as large as the anterior. The crop is well developed and is of the *Benthoctopus* type. The stomach has thin-walled upper and lower parts divided by a rather meagre muscular part. The crop and stomach contained Crustacean remains. The ink-sac is degenerate. The hectocotylized arm is short, about 64% of the longest arm. The end-organ is 4·5–2·5% of the arm. I have already discussed this organ fully (Robson, 1924, p. 207). The substance of that discussion is that the organ has the appearance of being undeveloped, though in its general form it is like that of Chun's specimen. The largest male of subsp. *capensis* is tolerably large, but its internal genitalia are poorly developed. It is not nearly as large as Chun's specimen, and I am inclined to think that the observed difference may be due to either age or seasonal change. The internal genitalia recall those of *E. cirrosa* (cf. Robson, 1924*a*, fig. 32).

Needham's organ runs straight into the penis, but there is a very small penial diverticle. Needham's organ is very small and the accessory gland appears to be rather undeveloped. Comparison of the male genitalia of this form with the immature organs of *E. moschata* (Marchand, 1907) shows at once that the peculiarities seen in *V. togata* are not of the same nature as those of the young *Eledone*.

*Remarks*.—Apart from the questionable difference in the hectocotylus I think this form shows some distinct differences from the typical form in the proportions of the web and papillation of the mantle. It is impossible to make sure whether in Chun's description of the funnel-organ he was describing the form seen and figured by myself.

### Subfamily 2. Bathypolypodinae, Robson.

Abyssal Octopodids which are always devoid of an ink-sac and in which the crop is usually reduced and sometimes absent. The eggs and vaginae are large and the spermatophores are large and few in number. The mantle-aperture is very narrow and the general habit is squat and short-armed.

### Genus **Bathypolypus,** Grimpe, 1921.

With the characters of the subfamily.

*Type of the genus.—B. arcticus* (Prosch).

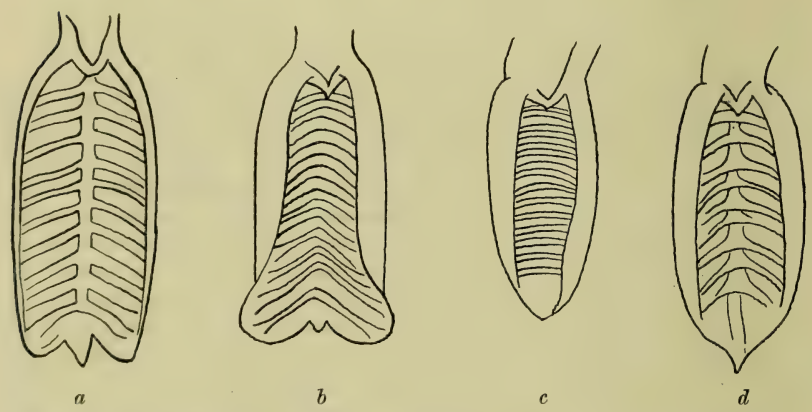



Fig. 53.—Hectocotyli of (*a*) *Bathypolypus obesus* and (*b*), (*c*) and (*d*) *B. arcticus*. (*a*, after Verrill; *b* and *c*, Brit. Mus. (C. 6 and C. 7), and *d*, Leiden Museum (Spitzbergen).)

### **Bathypolypus arcticus** (Prosch).

(Plate VI, figs. 1–2; text-figs. 30*b*, 53–60.)

? *Sepia octopodia*, Fabricius (1780, p. 360).
*Sepia octopus* (pars), Gmelin (1790, p. 3149).
? *Sepia Groenlandica*, Dewhurst (1834, p. 263).
(?) *Octopus granulatus*, Möller (1842, p. 4).
*Octopus arcticus*, Prosch (1849, p. 59, plate).
,, *grönlandicus* (= *O. arcticus*), Steenstrup (1856, p. 201, Pl. II, fig. 2).

*Octopus Bairdii*, Verrill (1873, p. 5, footnote).
„ „ *id.* (1873*a*, p. 394, figs. 76, 77).
„ „ *id.* (1874, p. 348, Pl. I, figs. 1, 2).
„ *groenlandicus*, Mörch (1877, p. 440).
„ „ Friele (1879, p. 284).
„ *Bairdii*, Sars (1878, pp. 339, 366, tab. 33 & XVII (radula)).
„ „ Verrill (1880*a*, p. 294).
„ „ Verrill (1881, p. 107, Pls. II & IV).
„ „ *id.* (1882, pp. 368, 421, Pls. XXXIII, XXXIV, XXXVI, XXXVIII, XLIX, LI).
„ „ *id.* (1884, p. 265).
„ „ *id.* (1885*a*, p. 563).
? *Octopus groenlandicus*, Dall (1885, p. 177).
*Octopus arcticus*, Hoyle (1886, p. 91).
„ „ Norman (1890, p. 466).
? *Octopus vulgaris*, Holt (1892, p. 246; *fide* Massy, 1909).
*Octopus arcticus*, Appellöf (1893, p. 1).
„ „ Lönnberg (1892, p. 6).
„ „ Grieg (1897, p. 24).
„ „ Posselt (1898, p. 269).
„ „ Nicholls (1900, p. 491).
„ „ Knipowitsch (1901, p. 538).
„ „ Friele and Grieg (1901, p. 123)
„ *Bairdii*, Joubin (1906, p. 8).
*Polypus arcticus*, Pfeffer (1908, p. 16, fig. 6).
„ „ Massy (1909, p. 6).
„ *faeroensis*, Russell (1909, p. 446).
„ *arcticus*, Russell (1909, p. 446).
*Octopus arcticus*, Odhner (1915, p. 238).
„ *bairdii*, Deriugin (1915, p. 554).
„ *arcticus*, Joubin (1920, p. 32, Pl. VII, figs. 4–5).
„ „ Bardarson (1920, p. 134).
*Bathypolypus arcticus*, Grimpe (1921, p. 300).
„ „ *id.* (1922, p. 40).
? *Polypus faeroensis*, Russell (1922, p. 5, Pls. 1 & 2).
*Polypus arcticus*, Russell (*l.c.*, p. 5).
„ „ Nordgård (1923, p. 5).
*Octopus arcticus*, Robson (1926*a*, *passim*).
*Polypus arcticus*, Grieg (1927, p. 16).
*Bathypolypus arcticus*, Robson (1927, p. 251, figs. 1–2).
*Octopus bairdii*, Tanasijcuk (1927, p. 217).
*Bathypolypus arcticus*, Massy (1928, p. 27).

*Type.*—In the Zoologisk Museum, Copenhagen. (? Syntypes.)

*Distribution.*—Arctic, N. and N.W. European and N. and N.E. American waters to as far south as S.W. Ireland and S. Carolina. (*a*) Arctic regions. i. Kola Bay (*c.* 69° 50′ N.), 84–13 fms. (Deriugin, 1915); Gulf of Kola (where ?), 169–27 fms. (Tanasijcuk, 1927); N. of Spitzbergen (81° 14′ N., 18° 30′ E.), 271 fms. (Knipowitsch, 1901); Spitzbergen, 227 fms. (Friele, 1879), in cod stomach (Grieg, 1926), 82–60 fms. (Odhner, 1915), 416 fms. (? 411, see discrepancy between Station

List and text) (Friele and Grieg, 1901); E. of Varanger Fjord (E. Norway), 150–85 fms. (Grieg, 1927); E. Finmark (Sars); N.W. of N. Cape, 191 fms. (Appellöf, 1893, Friele and Grieg, 1901); Lofoten Islands (Sars); N.W. Norwegian Sea, 350 fms. (Friele and Grieg, 1901). ii. (A) Davis Straits, Holstensborg (Greenland) ? depth; "Greenland" (Posselt, 1898); ? Pt. Barrow (N. Alaska), on beach (Dall, 1885); (B) Iceland (Bardarson, 1920); (*b*) N.W. Europe; Bohuslan, Kristineberg and Skagerrak (Lonnberg, 1892); Faeröe Channel, 345–632 fms. (Hoyle, 1886); Faeröes, 104–54 fms. (Grieg, 1927); Trondhjem Fjord, 164–54 fms. (Nordgård, 1923); Bergen Fjord and Sognesjøen, 200–350 fms. (Grieg, 1897, 1927); W. & S.W. Norway, 240–187 fms. (Joubin, 1920); W. of Shetlands, 287 fms. (Russell, 1922), 563 fms. (as *faeroensis* (*id., l.c.*)); E. of Shetland (Scottish Fishery Board), 686 fms.; N. of Shetlands (Scottish Fishery Board), 686 fms.; Aberdeen (Scottish Fishery Board), 55 fms.; ? Achill Head, Ireland, 220 fms. (Holt, 1892); S.W. Ireland, 250–680 fms. (Massy, 1909); S. Ireland (where ?), (Norman, 1909); (*c*) S. Greenland, Julianehaab, Ivigtut, 65° 36′ N., 56° 24′ W., and "Greenland" (Posselt); "Greenland" (very rare), (Mörch, 1877); (*d*) N.W. America: Miquelon Island, Newfoundland, south as far as latitude of Charleston–Savannah (S. Carolina–Georgia), 7–843 fms. (Verrill, 1873, etc.). The maximum of 843 fms. appears in the summary (1884, p. 265). So far there has been no record of this form eastwards of the Murman Coast. The various expeditions that have visited the Barents Sea, Franz Joseph Land, Nova Zembla and the north coast of Siberia have not obtained it. The exploration of the waters west and north of Davis Straits yielded only the very questionable record of Dall's from Pt. Barrow. The specimen noted by Dall was apparently identified by Verrill, who certainly should have been able to recognize his "*O. bairdii*." Nevertheless it is not described, and we should bear in mind that probably the waters of Alaska contain forms of true *Octopus* allied to the N. Pacific species described by Berry and Sasaki, with one of which *B. arcticus* might be confused. I do not assert that Verrill's identification is wrong; but I think it is suspect. *B. arcticus* was not obtained in the Pribyloff Islands during the Fur Seal investigations (Reports, III, p. 539). The species is not found south of a line drawn roughly from S.W. Ireland to Savannah in Georgia. This line coincides approximately with the northern limit of *Octopus* (s.s.) and seems to suggest that the two groups replace each other without very much overlap. In discussing the distribution of *O. vulgaris* (1929, p. 59, footnote) I commented on the curious disparity between the temperature at its northern limit in the E. Atlantic (isotherm of 11–10° C.) as opposed to that in the W. Atlantic (22°). It is now obvious that this anomaly is more apparent than real. Actually the bottom temperatures off S.W. Ireland and the southern part of Georgia are far more alike than those at the surface owing to the fact that, though in the latter the surface temperature is fairly high, the bottom water (that occupied by the adult animal) is very markedly chilled by the Labrador Current (Schott (1926, taf. XIV); Matthews (1914, Pl. 1 & foll.)).

*B. arcticus* is plainly a species of the edge of the continental shelf and the upper part of the continental slope. It ranges from quite shallow water down to a maximum depth of 843 fms. (Verrill). The average

depth would be about 200 fathoms. The very large number of depth-records available and the fact that none are in water of over 900 fathoms show that it is rather closely restricted to the continental slope.

*Specimens seen.*—(*a*) In Brit. Mus.

One (♀) from off Aberdeen (1927.6.14.1); one (♀) from the Shetland Is. (E) (1927.6.14.2); two (♀) from S.W. Ireland [C. 1–2], 1898.5.21.333–334; one (♀) from S. Ireland [C. 3], 1909.12.10.1; one (♂) from Trondhjem Fjord [C. 4], 98.5.21.345; one (♀) from Udsire Hole, Norwegian Coast [C. 5], 1927.3.18.1; one (♂) from "N. America" [C. 6], 98.5.21.340; one (♂) Martha's Vineyard [C. 7], 1890.9.15.81; two (♂ ♀) from the Faeröe Channel ("Challenger") [C. 8], 1889.4.24.35–6.

(*b*) In Z.M., Berlin.

One (♀) from Kola Bay (Murmansk); two (♂) from Vardo (Varanger Fjord); one (♀) from 71° 59′ N., 38° 0′ W. (off Murman Coast); two (♀) "Vega 1898, Deutsche Seefischerei"; one (♀) from Trondhjem.

(*c*) In R.M., Leiden.

One (♂) from Spitzbergen.

(*d*) In Marine Laboratory, Aberdeen.

Two adult (♂ ♀), 5 young (♀) from E. Shetland; one (♀) from N. Shetland.

(*e*) In Zoologisk Museum, Copenhagen.

One (♀) from Greenland (? syntype).

The following description is drawn up on the assumption that Russell's *P. faeroensis* is a form of *arcticus*.

*Description.*—The animal is of moderate size, rarely exceeding 60 mm. in mantle-length. The largest specimen known to me is one obtained by the "Vega" and now in the Berlin Museum. It measures 197 mm. over all and was in all probability longer (*c.* 215 mm.). One of Russell's ambiguous "*faeroensis*" was 48 + 170 mm. over all.

The body is ovoid or globular, its width varying from 61% to 102% of the length with an average of 90·1%. By far the greater number of individuals are wide. "*Faeroensis*" and two specimens, however ("Vega" (♀) Z.M., Berlin, and Verrill's smaller male (1882, p. 369)), are more oblong and the "Vega" specimen is distinctly narrow, its width-index being 63%. It is thus a very discontinuous variant from the usual squat form. The head is narrower than the body and ranges from 100–40% of the mantle-length with an average of 71·2%. Verrill's "original male specimen" (*l.c.*, p. 369) has a very narrow head (40%), if I am right in assuming that "length . . . exclusive of the arms" is equivalent to my apex-eye measurement, the standard of comparison used in discussing this dimension. The "Vega" specimen above mentioned is also very narrow across the head, a fact which suggests that these two forms are varietally distinct from, *e.g.*, the squat, broad-headed form (*e.g.* specimens in the British Museum from Trondhjem). The latter being also a male there is no question of sexual differentiation in this respect. The difference, however, may possibly be seasonal. The body sometimes exhibits a peripheral membranous expansion, and Verrill (*l.c.*, Pl. XXXIV, fig. 5) figured this expansion, and I have found it in four out of eleven specimens. It is well developed in two, very imperfect in the remainder. In none of the specimens is it uniform in size throughout its area. In two of the specimens it is continued past the eyes and runs up the web to join the

lateral membrane of the second arms. The chief interest of this structure centres in Naef's claim (1923, p. 675) that it represents a fin-rudiment (*i.e.* that it is homologous with the Decapod and Cirromorph fins). In discussing these (*l.c.*, para. 2) Naef first expressed doubt as to the homology with fins. In a footnote, however, he says, " die neuerdings bekannt gewordene *Stauroteuthis mawsoni* Berry 1917 (Austr., pp. 8–9) spricht allerdings eher dafür, die Seitenleisten für *reaktivierte Flossenrudimente* anzusehen." In spite of the fact that fin-rudiments are found in the embryo of *Octopus*, the position and form of these lateral membranes is certainly not very like those of the true fins of Decapoda. As far as I can ascertain, they are always mere cuticular ridges (" Hautkante " (Naef)) with no subjacent muscular basis, and, what is more to the point, at least in one specimen they do not occur in the Octopod fin-area ! While not denying that some part of these ridges may at the offset be vestigial fins, I think the second of the above-mentioned facts suggests that these folds are mainly secondary outgrowths of the skin. I have never found corresponding projections of the underlying body-musculature.

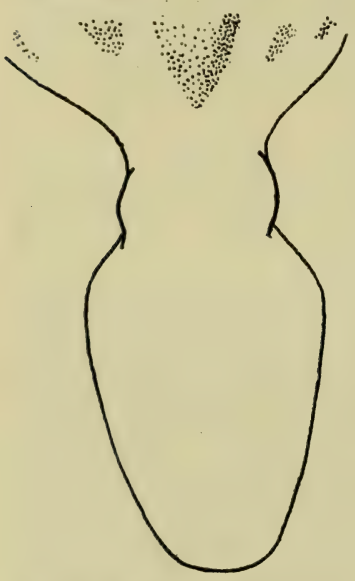


Fig. 54.—*Bathypolypus arcticus*, ♀. Outline of mantle. (Zool. Mus., Berlin.)

The surface-sculpture seems to occur in two definite phases :—(1) The dorsal surface of the web, head and arms is covered with simple or multifid warts, which are especially congregated around the eyes. Over each eye there is usually a prominent irregular (sometimes massive) cirrus. (2) The warts are less numerous and tend to be restricted to the antero-dorsal region. They are predominatingly of a stellate pattern, of which two main types seem to occur :—(*a*) a single multifid wart with a large central mass and smaller peripheral prominences ; (*b*) a main central wart surrounded by a number of *separate* smaller warts. (*b*) seems to be derived from (*a*) by the separation of the secondary smaller warts from the large central one. I have already described a similar evolution of the sculpture pattern in *O. rugosus* (1929, p. 68), and it is a very striking fact that this parallelism in sculpture-evolution occurs in these remotely allied forms. The various modes of sculpture are rather ill defined. The simple pattern and 2 (*a*) certainly occur together in the same individual. I am inclined to believe, however, that there is a varietal difference. The American forms which I have seen and those described by Verrill seem to have the first type almost exclusively, or 1 combined with (*a*). 2 (*b*) seems to occur most frequently in N.W. European waters, especially in the more northerly area. However, there is no clear-cut geographical segregation of pattern-types. Specimen C. 3 (Brit. Mus.) [S.W. Ireland] has 1 and 2 (*a*) combined like the American forms, and C. 1 (Brit.

Mus.) [same area] has all three types! 2 (*a*) is most clearly seen in "*faeroensis*."

The arms are sometimes subequal; sometimes they differ in length by as much as 25 mm. The order is rather irregular but seems to be

FIG. 55.—*Bathypolypus arcticus*. Outline of ocular cirrus. (Diagrammatic.) (Zool. Mus., Berlin.)

FIG. 56.—*Bathypolypus arcticus*. Funnel-organ (right member). (Gulf of Kola, Berlin Mus.)

1.2.3.4. They are relatively short, and the range is 67–78% with a mean of about 72%. The suckers are very small, the average diameter being 5·9% of the mantle-length with a range of 2·0–7·6%. As regards the structure of the suckers, I think that they tend to show a reduction in

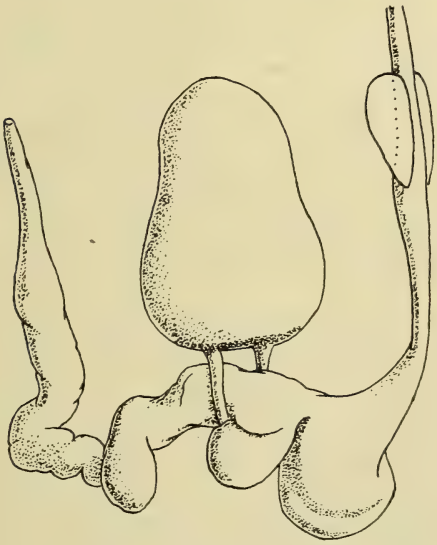


FIG. 57.—*Bathypolypus arcticus*. Alimentary canal.

the musculature. Normally developed suckers are certainly found (*e.g.* in the "Vega" specimen); but in two examples (C. 3 and C. 1) both circular muscles and basal part are poorly developed. The depth of the web varies from 24–46% of the longest arms, a figure which is highly suggestive of racial diversification. These divergences do not, however, follow geographical lines, as our forms with the lowest web are from the

Shetlands, S.W. Ireland and Martha's Vineyard (Massachusetts) respectively. The first four sectors tend to be subequal and the last is definitely shallower than the rest. The formula ABCDE is found quite often. The web is continued up the arms for only a slight distance. The funnel is free for about a third of its length; though in the "Vega" specimen and that from Vardo (Z.M.B.) it is free for 44% and 50% of its length. The funnel-organ usually is $\vee\vee$-shaped. The mantle-cavity is partly closed (B), there being usually some variation in this respect. The adhesive-apparatus is feeble, though the cephalic components are nearly always present. The gills have on an average 7–8 filaments. The inner demibranch always shows a decided, though not excessive, amount of reduction, and its longest filaments are only 74% of the total depth. The gill-surface is remarkably small. The *radula.* I have examined the radula of three specimens and as usual these organs show a good deal of individual variation probably due to differences in age. The variation

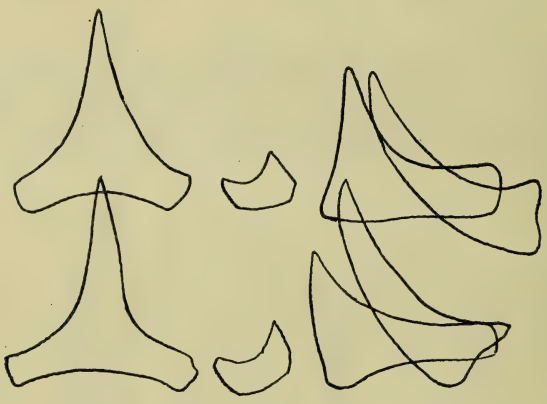


Fig. 58.—*Bathypolypus arcticus.* Radula.
(above) "Challenger"; (below) Martha's Vineyard (Brit. Mus.).

is best illustrated in text-fig. 58, in which a typical *arcticus* (C. 7) is seen along with a rather different form from the Faeröe Channel (C. 8). On the whole, the three radulae agree fairly well *inter se.* The rhachidian of the "Olga" specimen is rather narrower in the base, and it shows (possibly pathologically) a tendency to be tricuspid. The basal plate of the second lateral is thicker, and the third lateral is more slender. The maximum width of the rhachis is 23 : 27 of the height as opposed to 17 : 18 and 32 : 33 as in the other specimens. On the whole, the specimens I have seen agree fairly closely with Sar's figure (*l.c.*, Pl. XVII), less closely with Verrill's (Pl. XLIX, fig. 4).

*Reproductive organs.* A. *Male.*—The various parts of the vesicula are rather imperfectly distinguished; but, as in *B. valdiviae,* the third section is clearly differentiated. The appendix is well developed and there seems to be a second appendix, though the exact nature of this projection is vague. Needham's organ contains about 5–6 spermatophores, and is of the usual shape. The penis and its appendix form, as in *B. valdiviae,* a large kidney-shaped body. The system as a whole in specimens from

Martha's Vineyard (C. 7) and the Faeröe Channel (C. 8) agrees pretty closely with that figured by Prosch.

*The spermatophores.*—The diversity of the population under review is well indicated by the diversity in proportions, *e.g.* length of sperm tube to the rest of the structure. Prosch figures a very small sperm tube. This is again seen in a *faeroensis*-like specimen from Spitzbergen (C. 5*a*). In Verrill's figure and in C. 12 it is small but larger than in the preceding. In the typical squat form (*e.g.* C. 7), on the other hand, the sperm tube is very large and is actually longer than the rest of the structure. Russell (*l.c.*, p. 6) describes the spermatophores of "*faeroensis*" as abundant, adhering in strings and 2–5 mm. in length. This is so unlike those described for *arcticus* and seen by me that I think Russell must have been in error. The hectocotylized arm is about 75% of the first arms. The calamus is immediately adjacent to the last sucker. The ligula is very long in the Massachusetts (B.M.) specimen and that from Trondhjem (30–38%), shorter in that from Spitzbergen (17%) and still shorter in one of the Faeröe Channel intermediates (10%). Its sides are always inrolled and parallel to each other so that the organ is trough-like. There are 9–13 laminae copulatoriae. The distal extremity is either conical or truncate, but there is usually a small point.

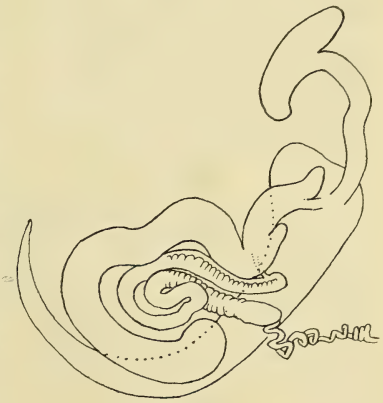


Fig. 59.—*Bathypolypus arcticus.* Reproductive organs (♂). (Brit. Mus., 89.4.24.35.)

B. *Female.*—The proximal portion of the oviducts are joined in the middle line. The "oviducal glands" are usually large and dark in adults, but in half-grown young specimens they are pale and relatively small. I do not think that the latter is necessarily a permanent feature. The proximal part of the distal oviduct is swollen.

*Habits, etc.*—The animal may be described as subabyssal. It is found in shallow water; but the average depth at which it has been obtained is about 200 fathoms, and it has been found at over 800 fathoms. Verrill (1882, p. 372 and foll.) described specimens kept in captivity. He notes that it is "probably largely nocturnal," that none of his specimens survived captivity for more than 4–5 days, that it rarely moved by means of the arms, but swam about readily and actively, and that the web was extensively used as an organ of locomotion, being "alternately spread and closed." I can hardly believe that the opening and closing of the web could supply much motive power. The stomach and intestine of a single specimen (C. 5) were opened and found to contain very much digested remains of Thecosomatous Pteropods and a few Crustacean remains.

*Remarks.*—The identity of the forms mentioned by early authors which might be referred to this species is very dubious. Fabricius' "*Octopodia*" might be an *Eledone*. Gmelin's *S. octopus* is a mixture of *Bathypolypus* and true *Octopus* ("mari mediterraneo, rubro, ad groenlandiam . . .")

(" verrucis sessilibus alternis in 2 series digestis "). Dewhurst's *groenlandica* is neither described nor figured. It is only said to differ " but little from *S. octopodia*." As it (*a*) comes from Greenland and (*b*) differs but little (!) from a true *Octopus*, perhaps we might reasonably give Dewhurst's name priority. But as it is an early, slightly ambiguous name it is better to retain *arcticus*. Moreover, it is by no means certain that *arcticus* is the only Octopod that Dewhurst had before him. Verrill (1882, p. 375) evidently thought, though on what grounds it is not clear, that *arcticus* and *groenlandicus* were different. From his description of the latter he may have been referring to a form of *piscatorum*. This is a very variable species, and it is very difficult to decide whether the European and American forms are conspecific and whether a form like Russell's *faeroensis*, which is very closely allied, should be treated as

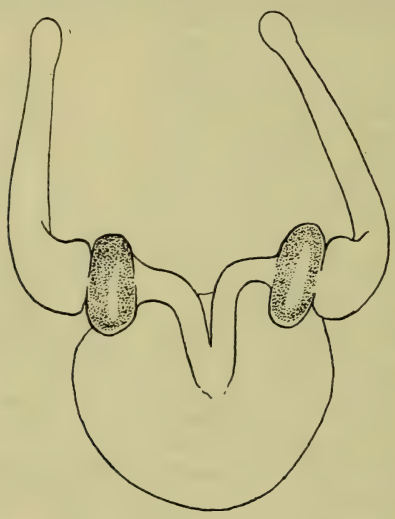


Fig. 60.—*Bathypolypus arcticus*. Female reproductive organs. × 3.

distinct. Prosch's original description is as follows :—The proportion between body and arm is 1 : 3. The suckers are small and widely spaced (the diameter of a sucker separating each). They are in two alternating rows. The first 4–5 are uniserial. They are moderately elevated and there is a maximum number of 80–85 on the dorsal arms. The web is deeper (*e.g.* than in *O. rugosus*) and its proportions are the converse of those of that species; thus it is deepest between the dorsal arms and shorter between the ventral pair. The brachial membrane is longest on the first arms. The visceral sac is ovoid " near the bottom dented like a heart " ( ? ventral or apical furrow). It is rough (but not shagreened). The sculpture ( ?) on the back and dorsal arms and membrane consists of " numerous hard and solid small lumps " more widely spaced anteriorly but " on the crown and body more regularly arranged in groups." Between the eyes is a " half circle of larger groups, each of them formed by a large central wart and several smaller in concentric rings." Over each eye there is a large warty cirrus. The granules are yellowish and they stand out against the reddish-violet ground-colour. There is one

difficulty presented in this description. The arms are said to stand to the body as 3 : 1, *i.e.* 75% of the total length. Now Prosch gives a small table of measurements (in mm.) which I transcribe.

| | ♂. | ♀. |
|---|---|---|
| Total length. . . . . | 175 | 175 |
| Visceral sac total length. . . . | 50 | 58 |
| 1st arms . . . . . | 145 | 135 |
| 2nd ,, . . . . . | 135 | 126 |
| 3rd ,, . . . . . | 125 | 110 |
| 4th ,, . . . . . | 122 | 103 |

Now it is plain that if we adopt the usual procedure of making the longest arms a percentage of the total we get not 75% but 82% and 77%. If, on the other hand, we deduct the length of the body from the total length we get (*e.g.* in the male) 125 mm. for the arm length (*i.e.*, 71%). What exactly is meant by " length of body " is not clear. Through the kindness of Mr. Sparck, Curator of the Zoologisk Museum of Copenhagen, I have been able to see the reputed type of Prosch's *arcticus*. This is a large female specimen labelled " Gronland M.R. Jorgensen 27.7.1840." I am not wholly sure that this is the type, as the chief measurements do not agree with those given by Prosch (*l.c.*, p. 58). The maximum overall length is 189 mm., not 175. The first arms are 135 mm., *i.e.* 71% of the total length. I hardly think the specimen would have changed so much with relaxation of the tissues, and the measurement I obtain is larger than that obtained by Prosch. Moreover, though the mantle has been opened its measurement is the same as Prosch found. In other respects the specimen agrees with Prosch's description. If it is the type it is a little unfortunate that it cannot be profitably employed owing to the ambiguity over the length of the arms. It thus follows that we cannot use Prosch's figures with any confidence as giving us exact proportions. As the arm-length is one of the characters in which Russell's species was said to differ, this is also unfortunate. It would be safer perhaps to accept Prosch's " 3 : 1 " as an indication that the arms are about 75% of the total length. Now if we regard Prosch's species as having

(1) arm with an index of 75% and in order 1.2.3.4,
(2) an ovate body,
(3) warty and stellate sculpture,
(4) web in order ABCDE,

it is plain that we are dealing with a form which in two respects differs from some of Verrill's *bairdii* and also from specimens referred to *arcticus* from European waters (*e.g.*, B.M. C. 7, C. 1). Verrill (*l.c.*, p. 368) speaks only of " small conical often irregular tubercles " and of " minute scattered papillae," never of stellate groups of large and small warts. The body is short and thick and figure 1 of his Plate XXXIII shows a broad squat, not an ovoid form. On the other hand, figure 6 of the Plate XXXIV shows a definitely ovoid form with a narrow head not unlike Russell's *faeroensis* (*l.c.*, Pl. 1, fig. 1). Again, some of the American forms and some European have much shorter arms than Prosch's form (see table). We thus arrive at the fact that there is, along with Prosch's species in the N. Atlantic, a broad and squat, very short-armed form with simple, non-stellate sculpture. This type is best realized in our

No. C. 3 from S.W. Ireland. On the other hand, there is the ovoid form with markedly stellate sculpture and long arms (75–77%) seen in Russell's *faeroensis*. This is nearer the type-form. Russell (*l.c.*, p. 7) also adduces (1) clearer distinction between head and body, (2) longer hectocotylized arm and (3) much shorter ligula, as proof of distinct specific status. The last three characters are unfortunately not described by Prosch. The latter, however, figures the male genitalia and spermatophores. The former agree in essentials pretty closely with specimens of (*a*) the squat short-armed form from the Faeröe Channel (C. 13) and (*b*) the same type from Martha's Vineyard (C. 7). The characteristics of the spermatophores may be thus summarized :—

| | Sac + oral tube : Sperm tube. | Ratio (Approx.). | False tube. |
|---|---|---|---|
| Prosch. . . . . | sac + oral tube > sperm tube | ( ?37 : 18) | not swollen |
| Verrill (Pl. XXXVI & text). | sac + oral tube > sperm tube | (35 : 25) | not swollen |
| B.M. C. 7 (Martha's Vineyard) . . . . | sac + oral tube < sperm tube | (26 : 24) | swollen |
| B.M. C. 12 (Faeröe Channel) | sac + oral tube > sperm tube | (15 : 35) | not swollen |
| C. 5*a* (Spitzbergen) . . | sac + oral tube > sperm tube | (15 : 43) | ? |

The hectocotylus in the American forms and our European series is alike in all respects save size, one of the latter having a relatively much smaller organ (only 10% of its arm). In *faeroensis* the organ is 11–12% and is broad and leaf-shaped and the calamus is remote from the last sucker.

Two questions thus present themselves : (1) is Verrill's *bairdii* the same as Prosch's *arcticus*, as has been so long held ? and (2) what is the relationship of the various forms that seem to come within the *arcticus-bairdii* complex ?

(1) (*a*) Verrill's *bairdii* was not homogeneous in body- and head-shape. His figure 1 on Plate XXXIII and text, p. 368, shows a broadly rounded form with the head almost as broad as the body. His figure 6 of Plate XXXIV and figure 8 of Plate XXXVIII show an ovoid, narrow-headed form. The latter agrees with Prosch's description. (*b*) If Prosch's type is to be regarded as having arms 75% of the total length, then from Verrill's figures (pp. 369–70) his *bairdii* (70–73) was rather shorter in the arm. (*c*) Verrill does not mention the *stellate* sculpture seen in *arcticus*, though he describes the warts, etc., of *bairdii*. (*d*) The web of *bairdii* is not described in detail. It is figured (*l.c.*, Pl. XXXIII, fig. 1) and that figure shows a web with formula D.B = C = E.A, while in Prosch's species A is most emphatically the deepest. I do not, however, attach much importance to the figure of the web. (*e*) The spermatophores in shape and proportion are very alike in the figures given by Prosch and Verrill. It must be confessed that the data for a confident verdict on this matter are not very ample. It is true that in view of subsequently acquired information, we feel that it is likely that the two authors had more or less the same form in mind. Nevertheless, in view of the great variability in the natural population, it is by no means excluded that the two authors may have used markedly divergent forms for their descriptions. This matter can only be settled by comparison of the types which I have been unable to make.

(2) A large number of forms have been ascribed to the *arcticus-bairdii* complex, and I have had under review a good number of specimens that obviously belong to the latter. It is really impossible to decide on the strength of a dozen specimens what sort of stable elements there are in a natural population of a large area like the North Atlantic. As already pointed out (Robson, 1929, p. 24), " the range of variation found in any sample of a species is dependent on the way in which the sample is taken." In this case our notion as to the status of the variants of *arcticus* must depend on what specimens we put into *arcticus*. That is why a larger amount of material is necessary before we can obtain any reasonable degree of certainty in this matter; for, the larger our number of individual cases is, the less susceptible to modification do our average (*i.e.* racial or specific) values become. In a case like the present one the only helpful thing to do is to describe the material or such important deviations as may occur in it and leave it for future investigators with perhaps a wealth of material to decide which are the most constant character-combinations.

1. *arcticus :* type form (Prosch). For characters see above.
2. *bairdii :* body ovoid or saccular, head wide or narrow, arms short, sculpture (?) warty, ligula at least $\frac{1}{3}$ of the arm, spermatophores with false tube not swollen, sac and oral tube longer than sperm tube, web (? 33) long.
3. *faeroensis* (Russell) : body ovoid, head narrow, arms (77–78) rather long, sculpture stellate, ligula short ($\frac{1}{8}$ of arm), web (24–28) shallow, spermatophores (?) see below.

4*a*. "*faeroensis*" ♀ (Scottish Fishery Board, 25/7/09) : body rounded, head narrow, arms short (71), web deep (36), sculpture as in 3.

4*b*. "*faeroensis*" ♀ (Scottish Fishery Board, 25/7/09) : body ovoid, head narrow, arms short (70), web very deep (46), ligula short (12), sculpture ?

5. Zool. Mus., Berlin : body narrowly ovoid, head narrow, arms very short (67), web very deep (44).

*Faeroensis* at the one extreme and the saccular form of *bairdii* seem to differ very markedly, while *faeroensis* (4*b*) exhibits a marked peculiarity in the web, and the Berlin specimen has excessively short arms. Among all these divergences I do not propose to recognize distinct forms. It remains for us to note that the typical *bairdii* form with saccular body, large ligula and short arms occurs in European waters (Trondhjem : Udsire Hole).

**Bathypolypus lentus** (Verrill) (? = **B. arcticus** (Prosch)).

*Octopus lentus*, Verrill (1880, p. 138).
,, ,, *id.* (1880*a*, p. 294).
,, ,, *id.* (1881, p. 108, Pl. IV, fig. 2).
,, ,, *id.* (1882, pp. 351, 375, Pl. XXXV, figs. 1–2; Pl. LI, fig. 2).
,, ,, *id.* (1884, p. 265).
,, ,, Appellöf (1893, p. 4).
,, ,, Grieg (1897, p. 24).
,, ,, Friele & Grieg (1901, p. 123).
*Polypus* ,, Pfeffer (1908, p. 17, figs. 7, 8).

*Polypus lentus*, Nordgård (1923, p. 6).
*Bathypolypus lentus*, Grimpe (1922, p. 40).
*Octopus* ,, Robson (1926*a*, *passim*).
*Bathypolypus* ,, *id.* (1927, p. 253, etc., fig. 1).

*Type.*—In U.S.N.M. (Holotype.)

*Distribution.*—(a) *N.E. America.* Grand Bank, Banquereau and St. Peter's Bank, Newfoundland, "S. of Newfoundland"; Le Have Bank, Nova Scotia; off S. Carolina (33° 42′ N., 76° 0′ W., 34° 39′ N., 75° 14′ W.) (Verrill), in 120–603 fathoms.

(b) *N.W. Europe.* Norwegian Sea (66° 41′ N., 6° 59′ E.), in 350 fms. (Appellöf, Friele and Grieg); Bergen, in 200–350 fms. (Friele and Grieg); Trondhjem (Nordgård), in *c.* 164 fms.

*Description.*—Verrill's type-specimen was a female. The body was broad with an index of 66 (78, from Verrill (1882, Pl. XXXV, fig. 2)). The head was said to be broad. From the figures given (p. 376) it had an index of 53, *i.e.* rather narrow, though in Plate XXXV, fig. 2, it is wider. The body is "depressed" and indented at the apex. A thin marginal membrane surrounded the body, attaining a width of 12 mm. posteriorly, where it formed a kind of tail. This membrane, which is probably adventitious (see p. 6), was "but little apparent" in other specimens. The arms are in the order $1 = 3.2.4$ or $2 = 4$ and are remarkably short, viz. 57–68% of the total length. The suckers are biserial as far as the base of the arms. The web, to judge from the figure, is about 33% of the arms, subequal in its sectors, except in E, which is shallower than the others, and is continued up the arms as a broad membrane. The surface of the female is not described except for the mention of a small conical cirrus over each eye. In the male it is smooth. The skin is soft and in some examples gelatinous. The colour is a deep reddish-brown, speckled with darker brown and "with many small roundish spots of whitish on the body and arms." The male specimen described does not differ in essentials from the female. It is more globular (width-index 82) and the head is wider (index 64). The arms are longer (68). The surface shows "a small number of minute white papillae sparsely scattered over the dorsal surface." The hectocotylized arm has 35 suckers and is 89% of the normal arm, which is longer than in *arcticus* by a good deal. The ligula, which is 39% of the arm, is very broad and spatulate. It exhibits 9 laminae which are very well developed, and ends in a sharp triangular lobe, and "from this lobe a broad groove runs along the lower edge of the arm to the margin of the web; where it terminates there in a distinct thickening of the bounding membrane."

*Remarks.*—Verrill (1882, p. 375) says that *B. arcticus* resembles this species. "but has a much larger and rough or lacerate cirrus above the eye." Appellöf, Grieg and Nordgård identify their European forms with so little hesitation that one would imagine there was no question of its distinct status. On close examination, however, it seems that *lentus* is extremely like *arcticus*, and, unless other authors and myself have drawn our definition of that species too generously, is probably conspecific. The points of difference are as follows:—(1) The arms in the female are shorter than in any *arcticus*. In the male, however, they are longer and easily within the range of *arcticus*. (2) The head is broader and longer

than in the average *arcticus*, but it can be matched in certain globular forms of that species. (3) The surface seems to be minutely papillate in the male. Sculpture is not mentioned in the female. This may be an important difference, but I have seen specimens of *arcticus* with very much worn evanescent sculpture. (4) The size of the hectocotylized arm exceeds that of *arcticus* quite considerably. (5) The ligula is only just outside the range of *arcticus* in length. On the whole it resembles that of *arcticus*, but the laminae seem to be fewer and coarser and the extremity is more pointed. I am a little inclined to disregard these differences, as forms which I do not hesitate to identify as *arcticus* tend to vary in the number of laminae and the form of the extremity. On the whole, I think that at least the male specimen described by Verrill was identical with *arcticus*. The status of the female depends on a critical examination of the type. It may prove to be an extreme variant of *arcticus*.

**Bathypolypus obesus** (Verrill) (? = **B. arcticus,** subsp.).

(Text-fig. 53.)

*Octopus obesus*, Verrill (1880, p. 137).
„ „ *id.* (1880*a*, p. 294).
„ „ *id.* (1882, p. 379, Pl. XXXVI, figs. 3, 4).
*Bathypolypus obesus*, Grimpe (1921, p. 300).
*Octopus obesus*, Robson (1926, *passim*).
*Bathypolypus*, Robson (1927, p. 253, fig. 1*c*).

*Type.*—In U.S.N.M. (Holotype.)

*Distribution.*—Nova Scotia (off Sable Island, in 160–300 fms.; (?) Banquereau in 150 fms.; both from stomach of Halibut) (Verrill).

*Description.*—The body is " oblong oval " and " stout," according to Verrill. He also describes it as " somewhat flattened above," which is not quite easy to reconcile with " stout." The eyes are very large, though the head is obviously narrow. The arms are short (66) and in the order 1.2.4.3. or 2.1. = 3.4. (? 1.2.3.4.), laterally compressed at the base and tapering to long slender extremities. The suckers are very small, the first 6–10 mainly uniserial. It is very doubtful if this is a permanent feature, as those on the second left arm are not thus arranged. The web seems to be rather shallow (? 27%). The hectocotylized arm is 71% of the first arms. Its ligula is 34% of the arm and is broad and thick. It is crossed by eleven curved laminae (the convexity of the curve directed proximally). They are joined by a mid-rib. The distal extremity is deeply indented and furnished in the middle line with a prominent point. The calamus is small and basal. The skin, which in the type was well preserved, seems to be devoid of sculpture and is soft and somewhat gelatinous. No ocular cirri were found, but the condition of the skin may account for this. The colour was mostly obliterated, but was apparently pale pinkish more or less thickly speckled with distinct reddish-brown spots.

*Remarks.*—Like *B. lentus* this may be a form of *B. arcticus*, but, as with that species, I am unable on the available evidence to determine its position more precisely. Verrill was unable to decide whether the smaller (Banquereau) example was referable to this species or to *lentus*. He says this species differs from " *bairdii* " and *lentus* in (1) its longer and

larger body and (2) the uniserial arrangement of the basal suckers. He also says that the ligula is " very much larger than in '*O. grönlandicus*' and considerably larger and flatter and more deeply trilobed at the end than in *O. bairdii*." Of these differences (1) and (2) are, I think, probably (but not certainly) unimportant. The mantle-length (72 mm.) certainly exceeds any *arcticus* I have seen, though the " Olga " specimen of the latter (66 mm.) is tolerably near it. But again the difference is not an important one. The uniserial arrangement of the basal suckers might be due to pressure or muscular distortion. I have actually seen specimens with normally biserial arms showing a very distinct uniserial arrangement. Finally, I do not think that the ligula alone constitutes a marked difference. It is said to be (*a*) more trilobate than that of *arcticus* and (*b*) considerably larger. Actually the extremity of the ligula varies very greatly in the *arcticus* population. In text-fig. 53 (p. 286) is seen that of a normal *arcticus* from Martha's Vineyard, Mass. The extremity of the ligula is very curious, the side lobes being very large and the median point very small. I also figure an undoubted *arcticus* with very acute point and well-developed mid-rib, and one with no mid-rib and obtuse point. Verrill is in error when he says the ligula of *obesus* is " considerably larger "; actually it is 34% of the third arm, while (1882, p. 369) he says the ligula of *arcticus* is about $\frac{1}{3}$ of the entire length (33%), and his figures (*l.c.*) give us actually $\frac{3}{8}\frac{3}{5}$ (= 38%). Undoubted specimens of *arcticus* in the British Museum have a ligula, the length of which is over 35% of the arm. On the whole, as far as Verrill's own views are concerned, I can find no critical difference between *obesus* and *arcticus*. It is very unfortunate that the skin was in bad condition, otherwise Verrill might have been more positive about the absence of cirri and sculpture. These features, combined with the low web and characteristic ligula, might justify us in treating this form as a distinct subspecies or race of *arcticus*. I do not, however, feel justified in placing it in the synonymy of *B. arcticus* until some information as to the type is available.

### **Bathypolypus sponsalis** (P. & H. Fischer).

(Text-figs. 61–63.)

*Octopus sponsalis*, P. & H. Fischer (1892, p. 297).
" " Fischer & Joubin (1907, p. 322, Pl. XXII, figs. 5–11).
Not = *Benthoctopus ergasticus*, Grimpe (1922, p. 41).
*Octopus sponsalis*, Robson (1926*a*, *passim*).
*Bathypolypus sponsalis*, *id.* (1927, p. 252).

*Type.*—In M.H.N., Paris. (? Holotype.)

*Specimens seen.*—Five (4 ♂ 1 ♀) in M.H.N., Paris, from type-locality.

*Distribution.*—Only known from W. Africa, 22° 57′ N., 19° 51′ W. (N. of Cape Verde Is.), in 508–454 fms. (muddy sand). (N.B.—P. & H. Fischer (*l.c.*, p. 298) give 932–1250 m.)

*Description.*—The body is short and broad (index 100–75) and the head is only a little less broad. The eyes are very large. Joubin and Fischer do not comment on this fact, but it is very striking. In the four specimens I have examined the eyes together comprise 47–50% of the body-area. This is excessively large (*e.g.* even if compared with *B. arcticus*). The funnel is very small in all the specimens examined. It

is largely adherent to the head. The funnel-organ is small and consists of two widely separated √ √-shaped pads. The visceral sac in two specimens has a narrow peripheral ridge. The mantle-aperture varies from AB–BC. The arms are probably in the order 1.2.4.3. and are short (68–77). The suckers are very small (3·3–5·5), alternating and sufficiently

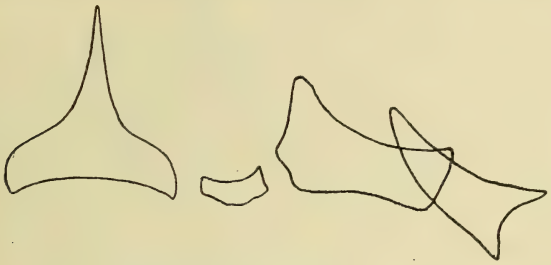


Fig. 61.—*Bathypolypus sponsalis.* Radula.

prominent. The web is subequal in its first four sectors, E being markedly smaller than the others. It is moderately deep (25–33). The musculature is firm and non-gelatinous except in one specimen. The sculpture of the surface varies. One of the specimens is quite smooth. In the

Fig. 62.—*Bathypolypus sponsalis.* Reproductive organs (♂). (M.H.N., Paris.)

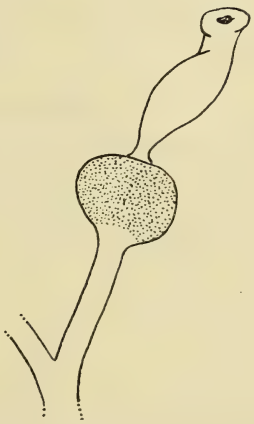


Fig. 63.—*Bathypolypus sponsalis.* Reproductive organs (♀). × 4·5.

others the eyes are surrounded by flattish blister-like pustules, which in two specimens extend over the head and more sparingly over the body. The colour was originally described as " purpureo-vinosum, concolor, maculis chromatophoris minutis tinctum." The mandibles are normal and *Octopus*-like. The *radula* has a unicuspidate rhachidian. The first lateral has a very low scarcely differentiated ectocone. The second

lateral is very remarkable. It has a very low stout cusp and a very short base. I think it is the simplest and least differentiated of any Octopod known to me. The same is true of the short, thick third lateral. There is only a very faint indication of marginal plates. There is no ink-sac and no crop, and the posterior salivary glands are small. The gills have about 7 filaments in each demibranch and the inner filaments are 67–70% of the outer in depth.

*The reproductive organs.* A. *Male.*—The penis and its appendix resemble those of "*B. grimpei*," though they are larger and narrower. Needham's organ is remarkably short, shorter, in fact, than in any form known to me. The prostate has an appendix. Needham's organ contained six spermatophores. These have a very large sperm tube which measures about 23 mm., the rest of the organ measuring only 11 mm. There is a marked swelling in the region which seems to correspond to the "oral tube." The hectocotylized arm is 71–54% of the longest arm. The ligula is 18–17% of the arm. It is provided with an enormous calamus which is over half its length. Its distal portion is rather triangular and is provided with 5–6 laminae. Its sides are heavily folded inwards.

B. *Female.*—The oviduct is almost as long as the vagina. The latter is short and swollen and has a wide terminal portion. The ovarian eggs are oblong and measure about 7·5 × 3 mm.

*Remarks.*—This is a very characteristic species. Its very large eyes and short body, the radula, hectocotylus and internal male and female genitalia differentiate it at once from *B. arcticus*, with which it seems to have some affinity. The five specimens which I have seen are tolerably homogeneous except in sculpture and arm-length. Grimpe (*l.c.*) queried whether it might not be identified with *B. ergasticus*. There are, however, many important differences (notably of funnel-organ and radula) between these forms.

**Bathypolypus salebrosus** (Sasaki).

*Polypus salebrosus*, Sasaki (1920, p. 182).
*Octopus* ,, Robson (1926, *passim*).
*Polypus* ,, Sasaki (1929, p. 99, Pl. VI, figs. 5, 6, text-fig. 54).
? *Benthoctopus salebrosus*, Robson (1929, p. 41).

*Type.*—In U.S.N.M., Washington. (Holotype ?.)

*Specimen seen.*—One (♀) in U.S. Nat. Mus. from the Sea of Okhotsk. (Paratype.)

*Distribution.*—Off Kinkasan (Japan), in 266 fms., and Sea of Okhotsk in 440 fms.

*Description.*—The body is subglobose (mantle-index 105–91) and the head is not much narrower than the body. The "neck" is imperfectly marked. The eyes are only moderately prominent. The arms are subequal and very short (73% of the total length in the paratype (the smaller specimen) according to my eye-extremity of arm measurement, less according to Sasaki's table). They are thick at the base and taper rapidly to the tip. They are entirely devoid of a brachial membrane. The suckers are small and do not display any abrupt increase. The basal cup is moderately thick-walled. The web is deep (33–28) and evenly developed in all the sectors except E, which is somewhat shallower than

the rest. The surface tissues are soft and loose but scarcely gelatinous. The sculpture consists of closely-set, roundish warts " which on the lateral and ventral surface of [the] body run together and arrange themselves in longitudinal lines " (Sasaki). The colour is (in alcohol) " light cardinal to claret throughout." The mantle-aperture is moderate (B or B–C). The funnel reaches beyond the level of the eyes. Sasaki (*l.c.*, p. 99) says it is short; but it is only short in relation to the very long web. It is rather oblong and tubular and (in the paratype) adherent for two-thirds of its length. The funnel-organ is according to Sasaki's figure ∧∨-shaped. In the paratype it is ∨∨-shaped. It is not very well preserved in this specimen, and it is just possible that it may be broken in the middle so as to appear double. There are 9–10 filaments in each demibranch. The *radula* has a well-developed rhachidian with a simple A type of seriation. There never seems to be more than one cusp aside and these are always very small. It is the simplest multicuspidate rhachidian that I know. The admedian is very small, its cusp low and the base very shallow. The base of the second lateral is also very shallow and short. The third lateral, on the other hand, is well developed, thick and straight. The marginals are only faintly indicated. There is no trace of an ink-sac. The vaginae (of the paratype which is immature with a very small ovary) are narrow and the oviducts are as long as the vaginae, an unusual feature. Sasaki (*l.c.*, fig. 54) figures them as shorter than the vaginae !

*Remarks.*—This species is unfortunately only known from two females, one of which is immature. Though coming from localities fairly distant one from the other, the two specimens agree very closely, and, as Sasaki (*l.c.*, p. 100) says, the species is very characteristic and unlike any other in the characters so far known. The question of the generic position is a little difficult. The short arms, rough skin and deep web recall the more characteristic members of *Bathypolypus*. The funnel-organ is, however, a difficulty. Sasaki describes and figures it as single (as in *Benthoctopus*), whereas in the paratype, in which the organ is not very well preserved, it is double. In the radula, though the rhachidian is multicuspidate and therefore *Benthoctopus*-like, it is of a very simple type. As the character of the funnel-organ is uncertain and the hectocotylus unknown it seems best to be guided by the decisively *Bathypolypus*-like characters and keep this species in that genus pending a more complete study.

**Bathypolypus valdiviae** (Thiele).

(Text-figs. 64–68,)

? *Octopus capensis*, Eydoux and Souleyet (1852, p. 11, Pl. 1, figs. 6–7).
*Polypus valdiviae*, Thiele (1915, p. 485, Pl. LXXX, text-figs. 52, 53).
,, ,, Robson (1924*a*, p. 667).
*Bathypolypus* ? *valdiviae*, *id.* (*l.c.*, p. 669).
,, *grimpei*, *id.* (1924, p. 208).
,, ,, *id.* (1924*a*, p. 663, Pl. II, fig. 10, text-figs. 37–41).
,, *valdiviae*, Massy (1926, p. 165).
" Undetermined Polypods," Robson (*l.c.*, p. 670).

*Type.*—In Z.M., Berlin. (Syntypes ?.)

*Specimens seen.*—(*a*) In Brit. Mus.

One (♂) (type of "*grimpei*") from the Coast of Natal; four (2 ♂ 2 ♀) from the same locality; one (♂) from Cape Town; one (♂) from Cape Point; two young (? sex) from west of Cape Town and Natal.

(*b*) In Z.M., Berlin.

Four (1 ♂ 3 ♀) from the Agulhas Bank.

*Distribution.*—Agulhas Bank in 273 fms. (Thiele); Coast of Natal and off Cape Town (Robson as "undetermined Polypod"), in 470–220 fms.; Cape Point, in 300 fms. (Massy).

*Description.*—The body varies very considerably in shape. Thiele (*l.c.*) described it as "deutlich breiter als hoch . . . der Kopf mit den grossen Augen eben so breit wie der Körper." His figure on Plate LXXX (fig. 2) shows a specimen about 37 mm. long (if natural size, as it seems to be) and about 27 mm. broad (index 73). This can hardly be described as "breiter als hoch"! The head is not "ebenso breit wie der Körper," but a good deal wider. Thiele gives some measurements (p. 486), but

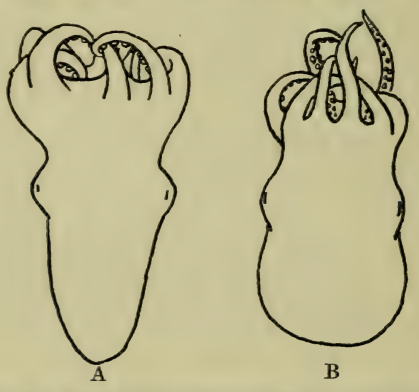



Fig. 64.—Young examples of (A) *Bathypolypus valdiviae* and (B) "*B. grimpei*." × ·25.

the points at which the mantle was measured are not indicated. I have measured three of what one may assume to be the syntypes and found them to be moderately wide (76–79) with the head (70–79), *i.e.* about as wide as the body on the average. In the type and all the other specimens of "*grimpei*" originally described by me the mantle is very wide (86–105), in the type attaining an index of 105. This is also found in one of the South African Museum specimens, and in all these broad-bodied forms the head is decidedly narrower than the body (77–90). There does not seem to be any sexual dimorphism involved herein; but I have only seen one adult female of "*grimpei*." In a young rather indeterminate specimen (Robson, 1924*a*, p. 670) there is a peripheral ridge. The arms are more or less subequal and very short (66–74). They are rather thick basally and gradually narrow to fine extremities. The suckers are very small (3·9–6·5), usually fairly prominent, but in most specimens are encased in the gelatinous integument. Viewed in section (fig. 65) they are at once seen to be less muscular than those of *O. vulgaris* or even *B. piscatorum*. The eyes are very large and remind one of those of *B. sponsalis*, though they are not so enormous as in that species. In one of the syntypes they are $\frac{1}{4}$ of the total length of body and head. In the type

of "*grimpei*" they are $\frac{2}{3}\frac{1}{3}$. The web tends to be subequal in the first four sectors, E being definitely shallower than the others. It varies in depth from 33 to 41%. The arm-membranes are only very imperfectly developed. The funnel in the syntypes is prominent and free for nearly half its length; that of the type of "*grimpei*" is involved in the tissues of the head. The funnel-organ is composed of two pads having the form seen in fig. 66. The adhesive-apparatus is weak, but distinct. The dorsal surface of the head, body and arms is covered with low, irregular multifid warts. These occasionally assume the pattern seen in *B. arcticus*, viz. a central boss surrounded by peripheral smaller warts. Usually the warts are more plentiful about the eyes and one or more here may assume the size of cirri. This feature is, however, of irregular occurrence and in the type of "*grimpei*" the cirri are absent. The colour is reddish-brown on the dorsum, lighter below. As stated by me, the type of "*grimpei*" is more evenly coloured as in the large female from Natal. The pallial aperture is narrow (B, B–A). The gills have about six filaments in each demibranch. The inner filaments are markedly reduced in length and are only 62% of the outer filaments. The gill itself (measured as suggested by me (1926*a*, p. 1340)) is under 11% of the mantle-area.

Fig. 65.—*Bathypolypus valdiviae.* Section of sucker. × 16. (Brit. Mus.)

Fig. 66.—*Bathypolypus valdiviae.* Funnel-organ (Left member). (Type, in Zool. Mus., Berlin.)

*Internal organs.*—The *mandibles* are well developed. The *radula.* I have examined that of the type of "*B. grimpei,*" which is on the whole not unlike that of the type of *B. valdiviae* figured by Thiele (*l.c.*, text-fig. 53). Such differences as undoubtedly occur seem to me to be negligible. The rhachidian is unicuspid and its base is wider than the height of the cusp (32 : 33). The admedians are very small, less than $\frac{1}{6}$ of the rhachidian in width, but the cusp is well developed. The second lateral is of a very simple character and approaches the third lateral in shape far more than in any other Octopodine. The third lateral is rather short. I could find no trace of marginals in "*B. grimpei*"; but Thiele figures them in the type of *valdiviae.* Both pairs of salivary glands are present, but the anterior are very small. The crop does not occur as a separate structure, but is merely a swelling of the oesophagus. It is, however, better developed than in *B. arcticus.* The *stomach.* In my account of *B. grimpei* (1924*a*, p. 665) I stated that the stomach consisted of two parts distinguished by their outer surface. Actually three regions are distinguishable in the stomach externally as well as internally. This differentiation is due to the interpolation of a thick-ribbed grinding portion between non-ribbed anterior and posterior portions (see Meyer, 1913, p.

34). The coecum is scarcely coiled. The first section of the intestine is thin walled and is succeeded by a thicker area. There is no ink-sac.

*The reproductive organs.* A. *Male.*—These have been fully described by me for "*B. grimpei*" (1924*a*, p. 666). Unfortunately I have not had access to any more mature males which I could dissect, so as to supplement my original account. The system is, as originally stated, very like that of *B. arcticus*. The *hectocotylus*. The ligula is 13–18% of the arm. It has been fully described by Thiele (*l.c.*) and myself (*l.c.*). In my original description of *B. grimpei* I stressed certain differences that are apparent between the ligula in that form and that of *B. valdiviae*. On comparing the type of the latter with that of "*grimpei*," I find that these differences are actually of subordinate importance, and may be related to the difference in gross size between the specimens and also to the fact that the ligula of the type of *valdiviae* is in a more contracted condition.

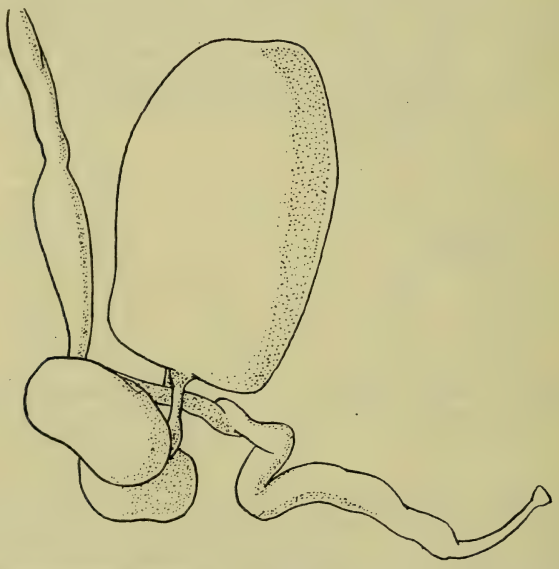


FIG. 67.—*Bathypolypus valdiviae*. Alimentary tract. × 3·5. (Brit. Mus., "*B. grimpei*.")

B. *Female.*—This system is remarkable for the very large size of the vaginae which are the largest found in any form known to me (text-fig. 68). The oviducal glands are small and the oviduct short. In neither of the specimens examined by me did I find any trace of a common oviduct.

*Remarks.*—This species is well described and figured by Thiele. The "Valdivia" specimens are smaller and obviously younger than those described by me as *B. grimpei*. I have little doubt, however, that the latter are conspecific with Thiele's species. In 1924 I was first of this opinion and then was impressed by the fact that between "*grimpei*" and *valdiviae* there were a number of minor differences which collectively seemed of importance. These nine differences are with three exceptions quite apparent, but I attach less importance to them, and in some cases the additional specimens I have seen have revealed intermediates. The differences in head- and mantle-width are striking, but not enough in

themselves to justify a specific distinction. The statement in my original description that the funnel-organ is " absent in the adult " is correct, but it is now known that this structure may be accidentally absent. The funnel-organ is very alike in the type of *valdiviae* and young specimens of *grimpei*. The alleged difference in the number of laminae copulatoriae of the ligula is more apparent than real. Actually there are four well-developed laminae in each form and in *valdiviae* a fairly well-developed fifth lamina and in *grimpei* a very weak additional lamina. On the whole, I think that the large male and female specimens of " *grimpei* " may constitute a well-marked subspecies, but they are too closely related to *valdiviae* to be treated as a distinct species.

*Variation.*—In the nine specimens examined the amount of variation is rather slight. The most noticeable feature is the occurrence of the

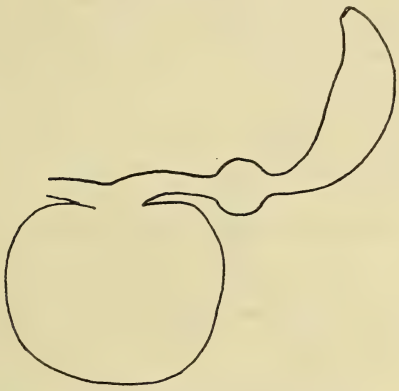


Fig. 68.—*Bathypolypus valdiviae*. Reproductive organs (♀). × 3·5. (Brit. Mus.)

broad-bodied (" *grimpei* ") and broad-headed forms. The arms, suckers, web and ligula vary but little. Certain growth-changes in the hectocotylus are noted by me (1924*a*, p. 664). The surface-sculpture varies in the extent to which the warts are subdivided and in the presence or absence of ocular cirri. Lack of cirri may be correlated with the broad head and body.

### **Bathypolypus** (?) sp.

(Text-fig. 69.)

*Octopus* sp. Hoyle (1886, p. 101).

Hoyle records some fragments of an Octopod taken in 1400 fms. at " Challenger " Stn. 184 (east of Cape York). The remains are quite undeterminable. I figure the mandibles.

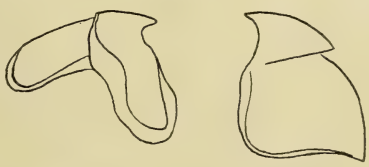


Fig. 69.—Undetermined Bathypolypod (?). Mandibles. × 2·25. (" Challenger," 1400 f.)

**Graneledone,** Joubin, 1918.

The radula exhibits archaic ( ? pre-Octopodid) traits in (*a*) the marked resemblance of the 2nd and 3rd laterals and (*b*) the unusually large size of the admedian. There is no ink-sac. The gill is very small. The hectocotylus is small but clearly differentiated into ligula and calamus. The penis has a large and saccular diverticle.

*Type of the genus : Eledone verrucosa,* Verrill.

It is a pity that the viscera of the very limited number of specimens representing this interesting genus are either not available for dissection or badly preserved, as some clearer light on its affinities might have been forthcoming. I think the character of the radula is undeniably archaic and not degenerate. The hectocotylus and penis are tolerably like those of *Pareledone.* The radula of one or two of the latter show more than a hint of the archaic features seen in *challengeri.* The reduction of the gill has gone further than in any known *Graneledone* and this organ is very like that of *Thaumeledone.*

The relationship between *G. verrucosa* (N.E. America) and *G. challengeri* (Kermadecs) is very interesting, and I am by no means certain as to the exact degree of affinity between them.

**Graneledone verrucosa** (Verrill).

(Fig. 70.)

*Eledone verrucosa,* Verrill (1881, p. 105, Pls. V, VI).
,, ,, *id.* (1882, p. 380, Pls. LII, LIII, = repetition of 1881).
,, ,, *id.* (1882*a*, pp. 393, 435, Pl. XLIV, figs. 3, 3*a* (repeats 1881)).
,, ,, *id.* (1884, p. 248).
( ?) Not *Eledone verrucosa,* Hoyle (1886, p. 104).
( ?) Not *Moschites verrucosa,* Hoyle (1904, p. 21).
( ?) Not *Eledone verrucosa,* Oliver (1915, p. 559).
*Moschites verrucosa,* Berry (1917*a*, p. 2, Pl. I, fig. 1).
,, ,, Joubin (1918, p. 1).
*Eledone* ,, Nielsen (1930, p. 3).

*Type.*—(?) In Peabody Mus., Yale University. (Syntypes ♂ ♀.)

*Specimens seen.*—One (♀) in Peabody Museum, Yale University ("Albatross," Stn. 2077).

*Distribution.*—Deep water off Halifax (N.S.), C. Sable and New York : 41° 33′ N., 65° 51′ W. (S. of C. Sable), in 810 fms. (Verrill, 1881); 39° 50′ N., 70° 11′ W. (E.S.E. of N. York), in 466 fms. (Verrill, 1881); Off Nantucket, "Fishhawk," Stn. 1123, in 787 fms. (Verrill, 1884); 39° 43′ N., 69° 21′ W.* (E.S.E. of N. York), in 1050 fms. (Verrill, 1884); 39° 41′ N., 69° 20′ W. (E.S.E. of N. York), in 1106 fms. (Verrill, 1884); 41° 09′ N., 66° 02′ W. (S. of Cape Sable), in 1255 fms. (Verrill, 1884); 38° 44′ N., 72° 38′ W. (S.E. of N. York), in 1209 fms. (Verrill, 1884); 42° 40′ N., 62° 49′ W. (S.E. of Halifax), in 797 fms. (Joubin, 1918).

Also :—Faeröe Is. (Nielsen) ( ?).

* This and the subsequent stations given by Verrill (1884) are to be found in Verrill (1885*a*, pp. 506, 507).

The record from off Cape Mala (7° 15′ N., 79° 36′ W., in 1020 fms. (Hoyle, 1904) is very dubious (cf. below).

*Description.*—The body is broadly ovate (original figure) or saccular and as broad as long (" Albatross," 2077). The apex is broadly rounded. The head is either as broad as, or rather less, wide than the body. The eyes are large but not prominent, and there is no neck. The arms are 85–72% of the total length, and the suckers are small and undifferentiated in size. Their diameter has an index of 6·4–5. The web is fairly deep (39–25 (?)) and bilateral. There is not much difference in the various sectors, but the formula is possibly C = D = B.A.E. The surface is covered with " prominent rough, wart-like tubercles and with a circle of the same around the eyes; four or five of those above the eyes are larger and more prominent." The specimen which I have seen agrees fairly closely with this description, except that there are only about 3 ocular cirri. The units of the main sculpture really consist of a main tubercle covered closely by 6–7 smaller knobs, which usually, but not always, encircle a slightly larger one. This sculpture differs from that of *challengeri* in that in the latter (1) the units are far more diffuse and less compact, (2) they consist of very many more and smaller subordinate knobs, (3) are very rarely stellate, and (4) the main base of the system is itself subdivided. The colour is a dark purplish-brown, and is darker below.

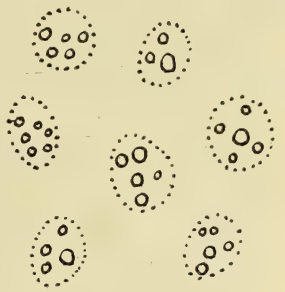


Fig. 70.—*Graneledone verrucosa* (" *media* "). Diagram of skin papillae. (Mus. Océanogr., Monaco.)

The mantle-cavity is very narrow (B–A). The gills have 7–8 filaments in each demibranch, the inner demibranch being little reduced. The funnel is wide at the base, moderately long and its extremity is small. The funnel-organ is double. There is no ink-sac.

*Remarks.*—The differences between this form and *challengeri* are discussed below under that species, and I believe with Berry that they should not be united.

Joubin (1918) claimed that his *media* more or less bridged the gap between them and it combined the hectocotylus of *challengeri* with the sculpture of *verrucosa*. This subject is discussed elsewhere. I do not think *media* really bridges the gap.

Hoyle's record (1904) from Panama is very doubtful. He says that one of the specimens " agrees very well with Verrill's description." No details are given by which we may check the identification.

### **Graneledone verrucosa** subsp. **media** (Joubin).

*Moschites verrucosa* var. *media*, Joubin, 1918 (25 Feb.), p. 1.
*M*[*oschites*] *media*, *id.*, 1918*a* (May), p. 39.
*Graneledone media*, *id.* (*l.c.*).
,, *verrucosa*, *id.*, 1924, p. 10, Pl. VI, figs. 15–17; Pl. IX, figs. 1–3.
*Moschites verrucosa* var. *media*, *l.c.*, p. 13.
*Graneledone media*, *l.c.*, p. 38.

*Type.*—In Mus. Oc. Monaco. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—" Princesse Alice " (3437.1913), 42° 40′ N., 62° 49′ W. (S.W. of Halifax); in 797 fms. " Chalut." Only known from the type-locality.

*Description.*—The body is very broad and squat, its width exceeding its length by a substantial amount. The general shape of the visceral sac is markedly rectangular, a very unusual feature in the group. The head is only a little narrower than the body. The proportions of the arms are uncertain. Joubin (1924, p. 13) gives R. 4312, L. 2 = 3, 1 = 4. They attain about 76% of the total length (G.C.R.). The dimensions of the suckers are not given. The web has the formula DECBA, A being markedly shallower than D, E and C. It is relatively deep (37% of the arms). The dorsal surface of head, arms (base) and body is covered with " papilles formées par la réunion de petites verrues juxtaposées." On examining the type I found that these warts are all more or less equal in size. Their arrangement is irregular and there are 3–8 warts in each group. These are absent on the ventral surface and on the free portion of the arms. The eyes are surrounded by a " cercle palpébral " of these warts numbering 12 in all, of which the two dorsal papillae are the largest. There seems to be two incomplete circles outside the main one. The pallial aperture is probably fairly wide (? B–C) (Joubin, *l.c.*, Pl. IX, fig. 2). Joubin emphasizes the fact that its edges are markedly swollen. The funnel is very small, and it has a square orifice. The general colour is " gris violet sur le dos, rouge violet gris sur le ventre, les bras un peu plus clairs à leur pointe due à un nombre immense de très petits chromatophores . . ." The internal organs are unknown.

The hectocotylus (Joubin, *l.c.*, Pl. VI, figs. 16–17) is about 4·9% of the arm and is very well developed. The arm (Joubin, *l.c.*, p. 13) is only 5 mm. less than the longest arm of the right side. It is 15 mm. shorter than its fellow of the left side which attains the maximum size, the hectocotylized arm being thus about 94% of the longest arm. The ligula is well developed and broad. The copulatory groove is rather shallow and the laminae copulatoriae are scarcely perceptible. The calamus is well marked and its basal channel has widely divergent edges. As far as I could make out from the type, without dissecting it, the ink-sac is absent.

*Remarks.*—It is a little difficult to make out Joubin's own views on the identity and relationship of this form. His most weighty pronouncement on the subject (1924, pp. 12–13) seems to have been that *challengeri* and *media* are varieties of *verrucosa*. Later on, however, he treated *media* as a distinct species.

As far as *challengeri* is concerned I think it is pretty clear that it and *media* are specifically distinct. The depth of the web, size and shape of the hectocotylus and funnel, width of the body and perhaps most marked of all, the difference in the pattern of the web are all considerable differences. The sculpture may be more or less alike, but it is closer and more bristly in *challengeri*. Lastly the circles of special circumocular warts are absent in the latter.

As for its relationship with Verrill's *verrucosa*, I can only express my opinion subject to the qualification that I have not been able to see the

type of the latter. From Verrill's figures and descriptions one would argue as follows. The body and head-shape and form of the hectocotylus are unlike those of *media*. The web length, according to the text, is a quarter of the length of the arms and therefore unlike *media*. In the figure, however, it is about 38% of the arms and thus like that of *media*. The hectocotylized arm is shorter in *verrucosa*, though not by a great deal. The pattern of the web (A very shallow) resembles that of *media*. The sculpture may also do so, though Joubin does not describe such definitely stellate warts as in *verrucosa*. The circumocular series of warts, though superficially alike from the two descriptions, do not seem definitely to be so. Joubin talks of a large inner circle of 12 warts and two fainter outer circlets, whereas in Verrill's figure there is a single circle of evidently larger warts which seem to be less numerous.

On the whole, the data available for coming to a decision are very inadequate, and I am inclined to retain *media* as a distinct variety of *verrucosa*, with the admission that the hectocotylus is notably different.

The following table of indices, etc., sets forth the relationships of these three forms :

| | Mantle. | Head. | Arms. | Gills. | Web. | Sculpture. | Hect. |
|---|---|---|---|---|---|---|---|
| 1. *challengeri* | 90 | 80 | 76 | 5–6 | 30 | See text | See text (3·3) |
| 2. *verrucosa*. | 94–58 | 92–84 | 85–72 | 8–7 | 39–25(?) | Unlike 1 | Unlike 1 (3·4–7·0) |
| 3. *media* . | 120 | 120 | 76 | — | 37 | probably = 2 | Unlike 1 & 2 (4·9) (more like 1) |

**Graneledone challengeri** (Berry).

(Text-fig. 71.)

*Eledone verrucosa*, Hoyle (1886, p. 104, not *E. verrucosa*, Verrill, *fide* Berry).

? *Moschites verrucosa*, Hoyle (1904, p. 21).

,, ,, Oliver (1915, p. 559).

*Moschites challengeri*, Berry (1916*a*, p. 49).

,, ,, *id.* (1917, p. 4, Pl. II, fig. 2).

,, *verrucosa* var. *Challengeri*, Joubin (1924, p. 13).

(?) *Graneledone challengeri*, *id.* (*l.c.*, p. 38).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—29° 45′ S., 178° 11′ W. (off the Kermadec Is.), in 630 fms. (volcanic mud); (?) off Cape Mala (7° 15′ N., 79° 36′ W.), in 1020 fms. (green mud). Only known from the type-locality.

*Description.*—The body has been very much distorted. I believe it was originally saccular and almost as wide as long. The head is only a little less wide than the body. The eyes, though large, are not very prominent. The arms are of moderate stoutness. They are presumably in the order 2.1.3.4.; but L. 2 being damaged, it is not possible to be precise. They are rather short (76%). The suckers are distinctly small for so large a specimen and do not exceed 7·0%. The lower chamber has a moderately thick base. The web is more or less equal in ABC and D, E being shorter than the others, and of moderate depth, viz. 30%.

The skin was covered on the dorsal surface of the web, head and body with exceedingly characteristic sculpture. This consists of masses of tubercles fairly closely-set and about 1·2 mm. in average diameter. They stand out very clearly from the surface and consist of irregular main warts studded with as many as 12–14 small white knobs. Berry (1917, p. 3) alludes to the units of sculpture as "stellate." In a sense he is correct in that each system of secondary prominences is a small constellation, but their arrangement is not star-shaped as is shown in *verrucosa* (Verrill, 1881, Pl. VI). Occasionally a unit is seen in which the secondary prominences are grouped round a median one. These, however, are uncommon. The colour (in spirit) is a dull brownish-purple. The mantle-aperture is distinctly narrow (B). The funnel is long and tubular, becoming gradually narrower towards the extremity. The adhesive-apparatus is not well preserved. The funnel-organ is VV-shaped, the anterior extremities of the limbs being narrow and pointed. There are 5–6 filaments in each demibranch, the gill being particularly small. The mandibles are normal and well developed. The radula (fig. 71) is certainly one of the most remarkable in the subfamily. The rhachidian is heavy and strong. I think it is actually unicuspid; but there is a

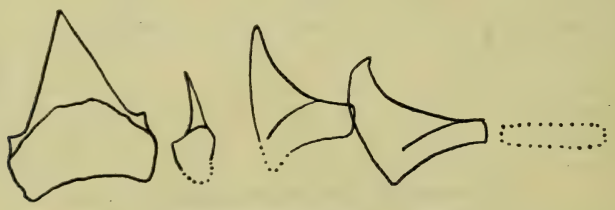


Fig. 71.—*Graneledone challengeri*. Radula. (Type.)

certain amount of asymmetry, and there is on some of the teeth an ectocone on one side only. The admedian is very tall and slender and has a narrow base. The second lateral has a very short base and is more like the lateral of a *Sepia*. The same is true of the heavy triangular third lateral. The morphological importance of these features is discussed on p. 9. The only other feature of the alimentary canal that can be made out is the absence of the ink-sac.

*Reproductive organs*.—The hectocotylized arm is 81% of the normal arms. The ligula is about 3·3% of the arm and has a wide and well-excavated copulatory groove. The calamus is relatively very large. It has a wide basal channel and it is rather acute. It is not unlike the organ of *G. media* (Joubin, 1924, Pl. VI, fig. 17), though it is shorter and the edges of the ligula are much thicker. The internal organs have been allowed to macerate so that their structure is not recognizable. The penis has a thick subcircular diverticle.

*Remarks*.—This form was originally identified with Verrill's N.W. Atlantic *verrucosa*. Berry (*l.c.*) rightly questioned this identification and gave it the name now used. Hoyle's record of *verrucosa* from West Colombian waters (1904) may be correct, but the specimens were not described. On the strength of a specimen obtained near the type-locality that combined the sculpture of true *verrucosa* with the hectocotylus of the Pacific *challengeri*, Joubin (1924, pp. 12–13) treated the latter and

his Halifax (Nova Scotia) specimen (*media*) as varieties of *verrucosa*. However, he was by no means certain in his mind on the subject as he treated all three forms as specifically distinct on p. 38 of the same work! Berry's comparison of photographs (1917*a*, p. 3) is of little value, because the photograph of the type of *challengeri* misled him into believing (*l.c.*) that the latter has stellate tubercles (see p. 312). There is no doubt that the two forms differ markedly in this respect. The form of the hectocotylus (from Berry's figures 1 and 2 and that of Verrill) is obviously different. The web (Verrill's figure) is deeper in *verrucosa*; but suckers, arms, and hectocotylus are more or less alike in size. I think on the whole we should uphold Berry's distinction. The comparison between *challengeri* and Joubin's *media* is equally difficult. The bodily proportions are certainly unlike, and in *media* the web is much deeper and of a different order. The sculpture of *media* (Joubin, 1918, p. 7) seems to be composed of 3–8 little warts which, from my examination, do not seem to be stellate as in *verrucosa*, but to form a loose constellation as in *challengeri*. The hectocotylus though not markedly different in size is different in form (perhaps in detail rather than in general shape and proportion of calamus to ligula). In *media* the hectocotylized arm is 94% ($\frac{2}{2}\frac{6}{8}\frac{5}{0}$) of the longest arm; in *challengeri* it is 81%, not a very considerable difference when shrinkage and accidents are allowed for. Other details are not available for comparison. It will be thus evident that we are hardly in a position to decide the relationships of the three forms. Nothing is known of the funnel-organ, radula and gills of *media*, and until such information is forthcoming it will not be possible to form any final conclusion. For the time being it must be granted that the two Atlantic forms have a good deal in common, though the hectocotylus is markedly different and both *verrucosa* and *media* exhibit about an equal amount of difference from and resemblance to the Kermadec specimen.

### (?) **Graneledone setebos,** n. sp.

(Text-fig. 72.)

*Moschites* sp. Massy (1916, p. 159, text-fig. 33).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—One (? ♀) from McMurdo Sound, Antarctica.

*Distribution.*—Cape Evans, McMurdo Sound, in a rock-pool. Only known from the type-locality.

*Description.*—Massy described "*Moschites* sp." from a single very mangled and decayed specimen obtained by the "Terra Nova." On examining this specimen I find that it is not possible to amplify her description to any extent as the specimen is in such a bad condition.

The body seems to have been very squat and broad (width-index 120). Even if we make allowance for the bad condition the arms were very short and probably under 60% of the total length. The suckers are rather wide (10%). The form, etc., of the web, surface-sculpture, colour, funnel and funnel-organ are unknown. Massy described the anterior and posterior salivary glands, which seem to have been normal in size.

*The mandibles.*—In the upper mandible the rostrum is nearly half as deep as the palatal lamella and projects freely behind the latter for a distance of 10–11 mm. There is no projection below the beak and

the anterior edge seems to have been almost vertical. There is no projection on the rostrum of the lower mandible.

The *radula* is the most remarkable feature of this species. The teeth, though differing in size as usual, are more of a size even than those of *G. challengeri*. The rhachidians are unicuspidate, the base being rather wider than the tooth is tall. The admedians are like small examples of the medians, having a tall central cusp. The second laterals, which have a large cusp and small base, seem to be like those of *G. challengeri*. The third laterals are very remarkable. As Massy says, they are not claw-like but made very much on the same plan as the median teeth. There is no trace of marginal plates. Massy (*l.c.*) seems to express some doubt that the teeth may be worn down as the result of age. I think it likely that the specimen may have been old; but in no old specimen that I have seen has wear produced the effect seen in this form. The effects of wear are quite different from these peculiarities; for example, they do not influence the position of the cusps nor the general shape, and could certainly not produce, in the third lateral, the change described above.

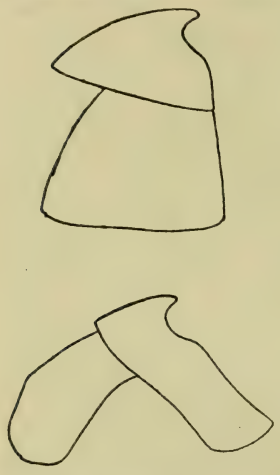


FIG. 72.—*Graneledone setebos*. Mandibles. × 5.

Massy makes the curious observation that the crop contained a considerable quantity of chopped-up green sea-weed. As the Octopoda seem to be wholly carnivorous she thinks it desirable to account for this and discusses several possible explanations. The chopping was apparently done by the mandibles and the weed shows no sign of having been rasped by the radula. I think myself that her suggestion that the animal, being confined in a rock-pool, had to make a meal of whatever was available is the most plausible. The absence of any trace of the action of the radula is very interesting and is commented upon elsewhere.

*Remarks.*—In spite of the very limited amount of information, I think we may safely regard this as a new species. When all possible allowance is made for the effects of age, the radula remains a highly characteristic and peculiar one, the simplicity and uniformity of the teeth being in my opinion definitely archaic. The radula has not a little likeness to that of a Decapod. This feature, the shortness of the arms and the form of the upper mandible collectively form a very characteristic and peculiar facies.

### **Thaumeledone,** Robson, 1930.

The radula is degenerate, being reduced to the rhachidian tooth. The gills have 5–6 filaments in each demibranch. The web is very deep and the arms short and subequal.

*Type of the genus.—Eledone brevis,* Hoyle (1885).

**Thaumeledone brevis** (Hoyle).

(Plate V, fig. 3.)

*Eledone brevis*, Hoyle (1885, p. 230).
,, ,, *id.* (1886, p. 105, Pl. VIII, fig. 7).
,, ,, Robson (1926*a*, *passim*).
Not *Moschites brevis*, Massy (1916, p. 158, figs.) (see p. 281).
*Moschites brevis*, Berry (1917, p. 13).

*Type.*—In Brit. Mus. (Holotype.)

*Specimens seen.*—Two (♀) in the British Museum (89.4.24.50–1).

*Distribution.*—Only known from the type-locality, off Monte Video, in 600 fms. on green sand.

*Description.*—The body is short, rounded and somewhat flattened dorso-ventrally. It is a little wider than it is long, and the head is slightly narrower than the body. The eyes are very large and amount to 40% of the capito-pallial mass. The arms are subequal, the first and second being a little longer than the third and fourth. They are 63% of the total length. The suckers are 5% of the mantle-length. They are closely set and deeply sunk in the arms. In section they are more or less normal; but the wall of the basal part is uniform in thickness. None of them is specially enlarged. The web has the formula A = B = C.D.E and is very deep (68% of the arms). I think Hoyle was in error in describing the surface as smooth. The small papillae behind the eye seem to have extended all over the front part of the dorsum. Probably all the dorsal surface was originally finely granular. There are three prominent cirri over each eye. Hoyle describes the colour as "dull purplish-grey inclining to pale ochre below." There is a very remarkable subcutaneous layer of purple pigment up the sides of the arms and round the mouth. This is not visible from the exterior except as a faint darkening of the web. The mantle-aperture is rather narrow (B). The funnel is short, small and pointed. The funnel-organ is represented by four long, separate strips of tissue, a very remarkable form reminding one of that seen in *Enoploteuthis margaritifera* (Jatta, 1896, p. 22). The rather similar organ with four separate pads seen in *Teretoctopus* should be compared. The gills are very small and globular and have 4–5 filaments in each demibranch. The mandibles are normally developed. The radula is represented by a single series of teeth, the rhachidian. These are unicuspid with rather stout mesocones and narrow bases. There are no traces of the other teeth. The crop is remarkably well developed. It is not, however, a diverticle in the oesophagus but a dilatation of the latter. The stomach seems to me to be less muscular than usual. The coecum shows very little spiral twisting. The first half of the intestine is dilated to form a capacious "third stomach." This is separated from the succeeding part by a narrow pylorus. The last section is wide and narrows abruptly to the anus. There are no valves and no ink-sac.

*The reproductive organs.*—Only those of the female are known. The vaginae are large and short. The system does not call for other comment.

*Remarks.*—The largest of the three specimens originally obtained was only 20 mm. long from eye to apex of mantle; it may therefore be a

young specimen. Its short arms and deep web are in keeping with this possibility. On the other hand, in the smaller of the two specimens still available, which is half the size of the larger, the arms are about the same size and the web is shallower. Now actually the tendency is for the arms to increase and the web to decrease in length with age, and certainly one would expect to find that a specimen twice as large as another had arms somewhat longer and web rather shallower. It would thus seem that the size of the arms and the web in the larger specimen is not necessarily indicative of immaturity. Another fact which points at least to its not being very young is the well-developed reproductive organs. Though it may not be fully grown, I think the larger specimen is more or less mature and its peculiarities are not to be discounted on the suspicion that it is as yet undeveloped. The radula with its single series of teeth is of course a very remarkable one. It is noteworthy that the rhachidian is not at all degenerate. Possibly taken in conjunction with the large crop, third stomach and rather ill-developed stomach, the degeneracy of the radula may indicate some peculiarity of the feeding-method. Nevertheless, the jaws are normal and the stomach contained the remains of Crustacea and (?) Polychaeta. Unless the animal remains were carrion and taken in with bottom débris I hardly think we can avoid concluding that this species is a normal carnivore. The large eyes, very much reduced gill, atrophied radula and (seemingly) specialized alimentary canal render this species one of the most interesting Octopodids. We should notice that it was not obtained at an excessive depth, though it is plainly adapted for a permanent existence in deep water. For Massy's "*M. brevis*" from Rio de Janeiro (1916) see p. 281.

**Thaumeledone gunteri,** Robson.

*Thaumeledone gunteri*, Robson (1930*b*, p. 392, Pl. IV, fig. 3; text-fig. 16).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—One specimen (♀) from N.E. of S. Georgia ("Discovery," Stn. 158, No. 2 ii).

*Distribution.*—Only known from the type-locality, 53° 48′ S., 35° 57′ W. (N.E. of S. Georgia), in 224–219 fms. Taken with a large dredge.

*Description.*—The body is globular and rather wider than it is long. The head is narrower than the body. The eyes are large and prominent. The arms are subequal and remarkably short (57%). The suckers are small and closely set. The first four sectors of the web are subequal, E being rather shallower than the others. The web is very deep, being about 60% of the arms. The surface of the web, head and body is closely covered by a number of characteristic warts. On the sides of the web and body they tend to be circular and bubble-like. On the anterior surface they are more irregular and often branched. In this area they are seen to be very clean cut and to stand out from the surface. As originally stated by me (*l.c.*, p. 393) they recall the similarly clear-cut warts of *Octopus pallida*, though they are not stellate. Joubin (1906, p. 6) says that in a form of *P. charcoti* some of the warts are probably branched. But the sculpture (Joubin, *l.c.*, Pl. 1, fig. 2) is really quite distinct in the two species. The funnel is short, narrow and pointed.

The funnel-organ is VV-shaped, the limbs being rather slender and pointed at each end. They are not unlike those of *P.* "*aurorae*" (Berry, 1917, fig. 14). The gills are very small. There are only 5–6 filaments in each demibranch. The inner demibranch is, however, very little reduced. The mandibles are normal. The radula exhibits the degeneration characteristic of the genus. It is represented by a strong rhachidian which is simple and unicuspid in pattern. Faint traces of admedians and of an oblong second lateral with a low cusp are to be seen. The posterior salivary glands are present and are tolerably well developed. There is no crop, the oesophagus showing a slight swelling in its place. The stomach is very small, but its walls are muscular and thick. There is no ink-sac.

*The reproductive organs.*—The ovarian eggs measure a maximum of 5·5 × 2·5 mm. The oviduct is extremely short. It is followed by a well-developed spermatheca and an enormous vagina. The latter is very much swollen at the proximal end, narrows down somewhat distally and expands again at the extremity. It recalls the similar type of vagina seen in *Bathypolypus arcticus* (Robson, 1927, p. 251, fig. 2*a*), but is far stouter and shorter.

*Remarks.*—This species is quite unlike *T. brevis* (*q.v.*) and cannot very well be mistaken for any other subantarctic species.

### **Bentheledone,** n. gen.

The external habit is like that of *Bathypolypus*, the arms being very short and the web deep. There is no crop and no ink-sac in the alimentary system. The radula combines specialized and degenerative traits (reduced rhachidian mesocone, admedian and second laterals) with primitive traits (simple rhachis and large, (?) functional marginals). The female reproductive organs exhibit (1) no common oviduct, (2) enormous vaginae and ovarian eggs over one-third the length of the mantle. The funnel-organ is simple and V-shaped (?) and the gill is very small.

*Type of the genus.—Eledone rotunda*, Hoyle.

For the time being I include Berry's *E. albida* here on account of its general resemblance to *rotunda*. The radula has some points of resemblance, but it is not wholly like that of *rotunda* in generic type. I also include provisionally in the definition the character of the funnel-organ as seen in *albida*, though it is not known in *rotunda*.

### **Bentheledone rotunda** (Hoyle).

(Text-figs. 73–75.)

*Eledone rotunda*, Hoyle (1885, p. 230).
,, ,, *id.* (1886, p. 104, Pl. VIII, figs. 4–6).
? Not *Moschites rotunda, id.* (1904, p. 21).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—One (♀) from the Southern Ocean (type).

*Distribution.*—Southern Ocean, 53° 55′ S., 108° 35′ E. (E. of Kerguelen and S.W. of Cape Lewin in W. Australia), in 1950 fms., on Diatom ooze (Hoyle); (?) off Valparaiso (Hoyle).

*Description.*—The body is broadly ovoid (perhaps not "spheroidal,"

(Hoyle)). The head is a good deal narrower than the body and the eyes are small (Hoyle's " rather prominent " is a little misleading), their total area being 10% of the mantle-area. The arms are subequal and remarkably short (66%) and stout. The suckers are very small (index 4·9%) and rather deeply-set. They differ but slightly in size. In section the wall of the chamber is seen to be only slightly thickened below. The web is deep (43%) and has the formula ADB = C.E. The surface is quite smooth and the colour was originally " dull purple." The mantle-aperture is narrow (B). The funnel is distinctly small and tapered. It is free from the head for a considerable part of its length. The funnel-organ and adhesive-organ are very badly preserved. There are 4–5 filaments in each demibranch. The inner demibranch is a good deal

Fig. 73.—*Bentheledone rotunda.* Alimentary canal. × 4.

reduced. The whole gill is very small and barely 12% of the mantle-area.

*Digestive system.*—The mandibles are strong and well developed (Robson, 1926*a*, p. 1346). In the work just cited I said that the radula is degenerate. Probably that statement is true on the whole. It requires some qualification, nevertheless. I think it would be correct to say that this radula combines primitive traits with others which are degenerate. It is certainly one of the most remarkable radulae that I have seen. It is not unlike that of *B. albida* (Berry, 1917, p. 17), though Berry's figure is by no means clear, and in two respects (the similarity of the triangular cusps of the second and third lateral in *albida* and the far larger mesocone of the rhachidian in the latter) it is definitely unlike that of Berry's species. The rhachidian has a very low cusp usually about $\frac{1}{2}\frac{7}{2}$ of the base in height. The admedian have hardly any sign of cusps at all and are thin and very weak. The second laterals have a very thin weak base and low, rather broad, cusp. The third laterals are much shorter than usual and the blade is set at a marked angle from the base. The most singular feature

is the high state of development of the marginals, which instead of being degenerate and evanescent are strong, obviously functional and partake somewhat of the character of the third lateral. I consider the character of the rhachidian is specialized (base) and primitive (no lateral cusps), that of the second lateral very degenerate, that of the third lateral

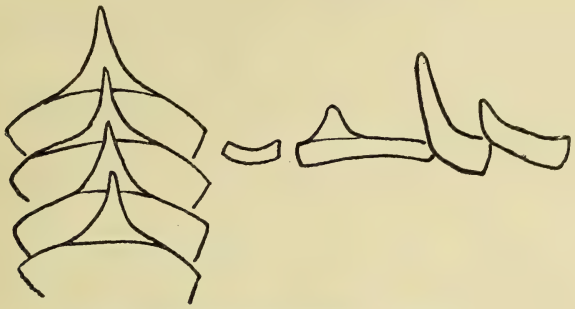


Fig. 74.—*Bentheledone rotunda.* Radula.

either archaic or degenerate and that of the marginal clearly archaic. I could find trace of neither crop nor ink-sac.

*The reproductive organs.*—The ovarian eggs are enormous considering the size of the animal; they measure 9·5 × 16·0 mm. The spermathecae are dark, fairly large, but not abnormal. The vaginae are the most remarkable of any that I have seen, being very short and enormously

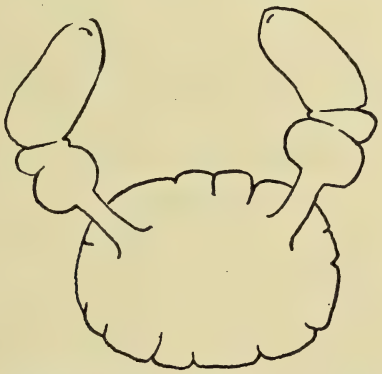


Fig. 75.—*Bentheledone rotunda.* Reproductive organs (♀). × *c.* 5.

expanded (fig. 75). There is a clearly indicated basal part. I feel pretty certain that the size of the vaginae is not adventitious. The oviducts are very short and seem not to have the common origin always found in this group.

*Remarks.*—This is a very remarkable and highly characteristic abyssal form. The very mangled specimen that was obtained off Valparaiso cannot be treated as conspecific. The only character worth attention in the remains is the web, which is a good deal shallower than that of the type. I think the same verdict must be accorded to the " *E. rotunda* "

obtained in 1° 7′ N., 80° 21′ W. (Hoyle, 1904) (see p. 321). Hoyle gives no description and the specimen is admittedly immature. I do not affirm that Hoyle's identifications are wrong, but for the time being the two records cannot be taken into those of *B. rotunda*.

**Bentheledone albida** (Berry).

*Moschites albida*, Berry (1917, p. 15, Pl. X, figs. 2–3; Pl. XI, fig. 4, text-figs. 6–9).

*Type.*—In the Australian Museum, Sydney. (Holotype.)

*Distribution.*—Only known from the type-locality, 64° 34′ S., 127° 17′ E., off Wilkes' Land, Antarctic, in 1700 fms., on thick ooze and rock. Temperature.—3° C.

*Description.*—This very interesting form is unfortunately only known by a single specimen. The body is a little broader than it is long, and "nearly round from the dorsal aspect." The head is short and broad but narrower than the body. There is little or no neck. The eyes are of moderate size. The arms are more or less subequal and attain a maximum size of 75% of the total length. They are "very stout, little attenuate." The suckers shown in the figure on p. 15 of Berry's description (not necessarily the largest) are *c.* 8% of the mantle-length. There are 57 suckers on 3 R. The web is deepest laterally, where it attains an index of 33+, and E is shallower than A. The surface is quite smooth and livid greyish-white (in alcohol). The mantle-aperture is fairly wide (? B–C, Pl. X, fig. 3). The funnel is "short and stubby" and extends "a little over the third of the distance to the umbrella margin." Its base is not very wide. The funnel-organ is large, of the shape of a thick-limbed V. The mandibles (Berry, *l.c.*, text-fig. 8) are "stout and black." It "diverges little from the regulation type" (Berry, *l.c.*, p. 17), though it must be noted that the beak of each mandible is far better developed and deeper than in, *e.g.*, *E. cirrosa* or *moschata*. The radula is "relatively delicate and transparent, taking stain (potassium bichromate) with difficulty." The rhachidians are simple, "hat-shaped" (?) with wide "flaring" bases. The first laterals are "weak, blunt, squarish, their outer angles more conspicuously developed than their inner." Actually they seem to lack all but the faintest trace of an entocone. The second and third laterals seem to have triangular cusps and to be more or less of a size(?). The marginals are not mentioned and are only vaguely indicated in the figure. Berry's figure (9, p. 17) omits the bases of the three laterals so that it is very difficult to understand what the teeth are really like. At present it seems as though this radula differs from that of *B. rotunda* in having (*a*) evanescent marginals, (*b*) similar second and third laterals, and (*c*) more or less of an entocone on the admedians. If Berry's figure is accurate the broadly triangular third laterals are unique in the Octopoda.

*Remarks.*—I include this species in *Bentheledone* for reasons already cited, though we do not know anything about the other parts of the digestive system and the reproductive organs. It differs from *B. rotunda* in the following respects: (1) its more globular shape, (2) paler colour, (3) longer arms, (4) the order of the web, and (5) sundry details of the

radula. The similarity between the second and third laterals of the radula, if accurately drawn in Berry's figure, is an archaic trait of high interest.

**Bentheledone** (?) sp.

Not *Moschites rotunda*, Hoyle (1904, p. 21).

*Distribution.*—Off Cape San Francisco, W. Colombia (1° 7′ N., 80° 21′ W.), in 1573 fms., on green ooze.

*Description.*—This form is only known from a single immature female. It was not described in detail. Hoyle identified it with the " Challenger " species (p. 317) " with some little hesitation." He stated that it differed only in (1) the occurrence of a shallow depression in the mid-ventral line, (2) the wider mantle-aperture, (3) the umbrella is proportionately better developed, and (4) the larger eyes. I have little doubt that this is the young of a totally distinct species.

## Family 2. Vitreledonellidae, Robson.

Bathypelagic Octopodids in which the inner demibranch of the gill is absent, and the digestive system is modified by the reduction in size of the salivary glands and liver. The crop is present as a thin vermiform coecum. The central nervous system is condensed. The radula tends to be like that of the Octopodidae. In at least one species a simple hectocotylus is found. The tissues are gelatinous and semi-transparent.

See Introduction (p. 48).

### Genus **Vitreledonella,** Joubin, 1918.

With the characters of the family.

*Type of the genus.*—*V. richardi*, Joubin.

**Vitreledonella richardi,** Joubin.

*Vitreledonella Richardi*, Joubin (1918*a*, p. 1, text-figs.).
,, ,, *id.* (1924, p. 15, Pls. I, III, IV, V, VI).
,, *richardi*, Robson (1930*b*, pp. 380).

*Type.*—In Mus. Oc. Monaco. (Holotype.)

*Specimen seen.*—One (the type).

*Distribution.*—Only known from the type-locality, Stn. 3223 (Monaco Expedition 1912), 30° 50′ N., 25° 43′ W., in 2899 fms.

*Description.*—The whole animal is gelatinous and semi-transparent. The body is short and saccular and under one-quarter of the total length. Its width is about equal to its length. The head is very short and is scarcely noticeable. The eyes are small, laterally flattened and are rather rectangular when viewed *en face*. The arms are in a poor condition and only five of them remain adherent to the head. Their length is difficult to determine. Joubin found that on the left side they measured 204, 156, 175 and 158 mm. respectively, though these figures are only approximate. They were probably 75–80% of the total length. The form of the web is uncertain. The deepest remaining sector (D) is about 30% of the longest arms. The web is quite transparent and is traversed by numerous muscle-fibres. There are 30 uniserial suckers on the longest arms. The adoral suckers are widely spaced and small. They increase in size towards the middle of the arm and the largest are nos. 12–14,

after which they become smaller and more closely arranged. Each sucker is implanted in a circular transparent boss at the apex of which is the aperture of the sucker. There appears to be no suctorial apparatus in the suckers.

The mantle-aperture is wide. The funnel is well developed and extends beyond the eyes. The funnel-organ is shaped like a wide ∧. There is no trace of a funnel-valve. The gills are very small and are only a centimetre in length. They consist only of the outer demibranch, which has seven filaments. There is a normal median pallial adductor. The external surface is covered with chromatophores which on the arms are more sparse than on the dorsal surface of the head and mantle.

*Alimentary canal.*—There is a single lip which exhibits 15 lappets. The jaws are weak and much flatter than is usual in the Octopoda. The rostral lamella of the lower mandible is deeper than the gular lamella. The beak is very small. These organs seem quite unsuited to the work of dismembering tough food. The radula has a rhachidian with two ectocones aside, a bicuspid admedian, the inner cusp being much larger than the outer, a unicuspid second lateral of more or less Octopodid form, a more or less straight third lateral and a lozenge-shaped marginal. There is a single median posterior salivary gland and no anterior glands. The crop appears to be represented by a thin vermiform coecum situated near the stomach. The stomach is divided externally into two parts. The spiral coecum is completely separated from the stomach by a short section of intestine of which it is a diverticle. The liver seems to be very much reduced in size. It is intimately associated with the ink-sac, which is almost as big as the liver and largely covers the latter over. It need hardly be pointed out that this is a very striking reversal of the arrangement usually found in the group. The intestine is very slender.

*The central nervous system.*—Joubin compares this system with that of *Eledonella diaphana*. The optic nerve is long and, as in *Bolitaena*, the peduncular ganglion is close to the optic ganglion. Joubin states that the cerebral, pedal, visceral and buccal ganglia are readily distinguishable; but from his figure I do not think they are as distinct as in the Bolitaenidae or Vampyromorpha. There is no distinct brachial ganglion such as is found in those groups. The white body is present, though very small.

*Reproductive organs.*—The single specimen known is a female. The female ducts are paired. The oviduct is long and slender. The oviducal gland is well developed. It is composed of a number of small pyriform subdivisions arranged around the central canal. Joubin, who examined the gland histologically, does not allude to the presence of spermatozoa, though their absence does not prove that the organ has necessarily no function as a sperm-reservoir. The vagina is slender.

*Remarks.*—For the relationship of this species to *V. alberti* and *translucida* see pp. 323–25. The anatomy has been described in detail by Joubin.

### **Vitreledonella alberti,** Joubin.

(Text-fig. 79.)

*Vitreledonella Alberti*, Joubin (1924, p. 38, Pl. II, figs. 1–2).
„ *alberti*, Robson (1930*b*, pp. 380–3).

*Type.*—In Mus. Océanogr., Monaco. (Holotype.)

*Specimen seen.*—One (the type).

*Distribution.*—Stn. 3128 (Monaco Expedition of 1911), 33° 40′–33° 52′ N., 19°–19° 16′ W., in 0–1914 fms.; Stn. 3131, 35° 9′ N., 21° 21′ W., same depth.

*Description.*—The animal is soft (? gelatinous) and semi-transparent. The body is saccular and as wide as long. It is relatively longer than in *V. richardi*. The head is very short as in *richardi*, the eyes rather larger, pedunculate and remarkably elongated. They are directed far more dorsally than in *V. richardi*. The arms are subequal and about 72% of the total length. The web is in a poor condition and its plan and depth are very uncertain. Between the dorsal arms it seems to extend to the level of the third sucker. In sector B there is no web (? destroyed); in C and D it reaches the level of the fourth sucker and in E it reaches that of the second. On the first arm the first five suckers increase in diameter outwards from 1·5 to 3 mm., the sixth to 4 mm., the seventh to 5·5 mm., the eighth to about the same, the ninth is about 5 mm. From that point there is a series of thirteen which gradually diminish in size and become closely serried. On the second arm the ninth sucker is the largest and is about 9 mm. in diameter. On the third arm the arrangement is the same, though the suckers are smaller and on the fourth arm the largest suckers are still smaller. As in *V. alberti* the suckers are planted in a large cutaneous boss. The mantle-aperture is very wide. The funnel is shorter than in *richardi*, but thicker. Its external aperture is edged by a bilobed membrane. In the type immediately behind the "lower lip" (?) there is a prominent fold. There is little information available concerning the other structures. There seem to be two lips around the mouth, a feature not found in *richardi*. The gills are smaller even than those of *richardi*. These, as Joubin says, give one the impression of being of little functional importance. The sex of the available specimens is unknown. Besides the type another specimen was obtained. This is in a very bad condition and it is not certain if it belongs to the same species. The gills of this example are so small that Joubin had some difficulty in finding them. It seems to have a funnel-organ of the same shape as in *V. richardi*. The ink-sac seems to be very small.

Fig. 76.—*Iapetella diaphana* (?).
(From a sketch of a specimen in Mus. Océanogr., Monaco.)

*Remarks.*—I think Joubin was right in distinguishing this species from *V. richardi*. The size of the body, the form of the eyes, the relative order and size of the arms (?), the arrangement of the suckers, the size of the gill and probably the depth of the web seem to differentiate them. The two species were found more or less in the same area. It is a pity that the sex of the specimens of *alberti* is unknown, as it is possible that it may be the male of *richardi*, though I hardly think that this is likely.

**Vitreledonella ingeborgae,** Joubin.

*Vitreledonella Ingeborgae,* Joubin (1929*b*, p. 16, text-figs. 40–41).
,, *ingeborgae,* Robson (1930*b*, p. 380, etc).

*Type.*—In Carlsberg Laboratory, Copenhagen. (Holotype.)

*Distribution.*—Only known from the type-locality, 36° 36′ N., 26° 14′ W. (off Azores) (" Dana "), in 1094 fms.

*Description.*—The body is gelatinous, almost transparent and of a general rose-lilac colour, with a good many chromatophores, which are especially dense on the dorsum. The head is very short and, as Joubin says, the arms seem to come directly off the visceral sac. The latter is as broad as long. The eyes are small, oval and dorso-lateral in position. There is, as in *V. richardi*, a small " orifice palpébral." The arms are in the order 1.3.2.4. (? 1.2 = 3.4). and 72% of the total length. The suckers within the area of the web are small and separate from each other and are carried on a transparent boss. Before the edge of the web they become sessile. The first 7–8 are very small. From the eighth outwards they become suddenly larger and closer together. There are 7 big suckers, and numbers 10–13 are the largest. The series is completed by three moderate, 3 small and 6–7 very small ones. All the latter are in contact with each other. The web seems to be about half as long as the arms and to be of the form A.B.C.D.E. The pallial cavity is very wide. The funnel is said to be " très développé," but in fig. 40 it looks short and (the head being tilted) scarcely passes beyond the level of the eyes. There seems to be a horseshoe-shaped funnel-organ. The gills are very small and are only about $\frac{1}{4}$ of the mantle in length. The mouth is surrounded by a highly developed peribuccal ring of suckers. The other organs are not described. The animal seems to have been viviparous. Joubin found 540 embryos of about 5 mm. in length, which seem to have been accommodated in the mantle-cavity. In the angle between the first and second arms on the left Joubin found three embryos in a closed pouch of the skin. These were rather less advanced in development than the others; but quite normal and showed signs neither of decomposition nor resorption, though they were completely covered over by the maternal skin. Joubin could find no communication between the pocket that contained them and the exterior.

*Remarks.*—This species is well distinguished from the three others as far as I can make out. It should be noted that the proportions given must be subject to some uncertainty. Joubin says the visceral sac is " 30 mm. . . . de haut." Actually the size of the figure does not agree with this. From the eye to the apex it measures 78 mm. and from the mantle-edge *c.* 58. Whichever length we take this is much larger than the length cited, and yet the figure is actually said to be " réduit de un tiers " [sic !].

**Vitreledonella translucida,** Robson.

*Vitreledonella translucida,* Robson (1930*b*, p. 380, text-figs. 7–10).

*Type.*—In Brit. Mus. (Coll. R.S.S. " Discovery "). (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Only known from the type-locality, Stn. 273, R.S.S. "Discovery," 9° 38′ S., 12° 42′ E., in 0–125 fms. Taken in a young-fish trawl.

*Description.*—The tissues of the animal are of a delicate consistency and semi-transparent. The body is narrowly ovoid, its width being 68% of the length. The head is, as in the two preceding forms, very short. The eyes are small, prominent and directed somewhat dorsally. The arms were rather badly damaged, but seem to have been in the order 1.2.3.4. They are relatively very short, being about 54% of the total length as compared with 72% in *ingeborgae*, 78–80% in *richardi* and 72% in *alberti*. The arms, though delicate and transparent, are thick and clumsy. Towards the extremities they taper rather rapidly. The total number of suckers is uncertain, as those at the tips of all the arms have been lost. There may have been about 20 in all. On most of the arms there are seven to eight small and very widely spaced suckers, followed by about four much larger and more closely placed ones. These are probably followed by about 8 much smaller ones. As in *richardi* and *ingeborgae* the suckers are implanted in gelatinous bosses. They are simple and thin-walled and show very little structural differentiation. The web has been partly destroyed and its exact form is uncertain. It may have been about one-third of the arms in length.

The mantle-aperture is wide; the funnel is short and stout. The funnel-organ is of the same general shape as that of *richardi*, but it is more flattened out. There are seven filaments in the outer demibranch. The inner demibranch is, as usual, absent.

The *radula* has a rhachidian with asymmetrically disposed ectocones, which have an *Octopus*-like seriation. The admedian has a large median mesocone, small ectocone and a shallow base. The second lateral has an obvious inner heel. The third laterals are long and slender, the marginals oblong. The radula differs in several particulars from that of *V. richardi* (Joubin, *l.c.*, Pl. V, fig. 12) and is distinctly *Octopus*-like.

*The hectocotylus* (?).—The third arm of the left side seems to be hectocotylized. It is shorter than the other arms, and on one side there is a narrow folded membrane forming what seems to be a seminal canal. At the extremity a number of the suckers are closely set and flattened against one another. Just short of the tip there are no suckers and there is a faintly grooved swelling followed by a point. The presumed seminal channel terminates in the swelling. The general structure is very like that of *Amphitretus pelagicus* as figured by Sasaki (1917, fig. 2), though in that form there are some paired suckers beyond the swelling.

*Remarks.*—The affinities of this form have been fully discussed by Robson (*l.c.*, pp. 382–3). It is quite clearly distinguished from *richardi* and *alberti*. Its relationships with *ingeborgae* are rendered a little uncertain owing to a discrepancy between Joubin's text and his figure. There are, however, differences between the two species, which are not affected by this discrepancy.

### Tribe 3. **Ctenoglossa,** Naef.

Gelatinous or subgelatinous Incirrata with multicuspidate rhachidian and lateral teeth. There is no adhesive-apparatus, funnel-valve, water-

pores or shell-vestige. Some ganglia of the central nervous system are more or less distinct. The crop is very large and the inner demibranch is reduced to half the normal size. There is no sexual dimorphism. The suckers are uniserial. The water canals are absent (?). The posterior salivary glands are larger than the anterior.

### Family 1. Bolitaenidae (Chun) Naef.

The mantle-aperture is widely open and the ventral edge of the mantle is free. There is no end-organ on any of the arms in the male. The funnel organ is Λ-shaped.

In 1859 Steenstrup published a short diagnosis of *Bolitaena* without describing any species. The diagnosis was very vague and merely referred to the slight development of the suckers, the gelatinous consistency of the tissues, slight curvature of the jaws and serial repetition of the radular teeth. In 1915 (*l.c.*, p. 491) Thiele obtained the two original specimens on loan from the Zoologisk Museum, Copenhagen, and published an expanded description (with figures) of them. I have now obtained the loan of these specimens from the Zoologisk Museum, Copenhagen, and give as full an account as possible below. In 1886 (1886, p. 16) Hoyle gave a short description of *Bolitaena microcotyla* (Steenstrup MS.) "from notes made in the Copenhagen Museum" (Hoyle, 1904, p. 8), but made no material addition to our knowledge of the genus. In 1904 (*l.c.*) he described a specimen from the Pacific as "*Bolitaena microcotyla*"; but this (p. 220) is undoubtedly referable to the Alloposidae. *Bolitaena* now turns out to have been an Eledonellid with a long optic nerve, the peduncular ganglion of which is situated close to, but not in contact with the optic ganglion. The only two specimens known are most unfortunately both females, so that the nature of the enlargement of the suckers in the male (so-called "hectocotylus"), an important diagnostic feature, is unknown. The gill has five filaments and the funnel-organ is a remarkably elongate with very close arms. How far *Bolitaena* is really distinct from *Eledonella* is very hard to say. The situation of the peduncular ganglion and the funnel-organ are distinctive, and until we know something of the male characters it is better to keep it as a separate genus with *microcotyla* as its type. How far we are entitled to include in the description of *Eledonella* the full anatomical account of *pygmaea* given by Thiele (*l.c.*) is discussed on p. 331.

We must now consider the status of *Iapetella prismatica* and the so-called *Eledonella diaphana*. In 1885 Hoyle described *Iapetella* with *I. prismatica* and *diaphana*. In 1886 he retained *prismatica* in *Iapetella*; but transferred *diaphana* to *Eledonella*. He originally distinguished the two genera on the ground that *Iapetella* lacked a median septum and possessed a funnel-valve. Later (1904, p. 23) he confessed that he was mistaken about these features and withdrew them from his diagnosis. The types of both *prismatica* and *diaphana* are, however, in too bad a condition to allow me to decide if they are otherwise distinct. Even the character of the optic nerve in *prismatica* is uncertain. In the circumstances it seems to me better to treat *prismatica* and *diaphana* as members of the same genus, *Iapetella*, which obviously has a prior claim over Sasaki's *Chunella* proposed for it in 1920. If, however, it be ultimately

shown that there are three genera involved, and that *prismatica* is not congeneric with *diaphana*, then *Chunella* will be available for *diaphana*. This arrangement, which is founded mainly on the position of the pedunculate ganglion, is provisional. *Bolitaena microcotyla*, indeed, seems to differ quite markedly from *Iapetella* and *Eledonella*. But I admit that the position of *B. massyae* and *ijimai* is by no means certain and their inclusion in *Bolitaena* is somewhat arbitrary.

**Bolitaena,** Steenstrup, 1859.

The optic nerve is long and the peduncular ganglion is adjacent to the optic ganglion. There are five filaments in the demibranch.

*Type of the genus.*—*B. microcotyla*, Hoyle.

I include herein my *Eledonella massyae* and Sasaki's *E. ijimai* on account of the position of the peduncular ganglion.

**Bolitaena microcotyla,** Hoyle.

*Bolitaena microcotyla*, Hoyle (1886, p. 16).
Not ,, ,, *id.* (1904, p. 9).

*Type.*—In the Zoologisk Museum, Copenhagen (syn-types).

*Specimens seen.*—The syn-types.

*Distribution.*—N. Atlantic 34° N., 32° W. and 2° N., 21° W. (Copenhagen Museum).

*Description.*—This is based on the smaller of the two original specimens, the larger being too mangled for proper description. The body is of the somewhat elongate-ovoid shape characteristic of the family. It measures about 34 × 21 mm. The head is remarkably short. It is impossible to give the precise dimensions of the arms, as some of them are incomplete and others are distorted. The longest may have been about 30 mm. long or about 46% of the total length. The deepest sector of the web is 36–40% of the arms; but its size and shape are very uncertain. On the longest arms I found 13–14 suckers. The distal 3–5 mm. of each of these arms is devoid of suckers, but their absence may be due to accident. The suckers are small and rather more than their diameter apart. The colour was, according to Hoyle (1886), reddish purple. The tissues are gelatinous. The mantle-aperture is wide, the funnel small but prominent. The funnel-organ is elongate and its arms are closely applied one to another, thus differing from the form seen in the other members of the family. There are 5 filaments in the outer demibranch. I was unable to make certain how much of the inner demibranch remains. The median adductor is present. The optic nerve is long (longer indeed than is figured by Thiele) (*l.c.*, fig. 58), and the peduncular ganglion is close to the optic ganglion. The radula (Thiele, *l.c.*, fig. 57) differs markedly from that of *Eledonella* and *Iapetella* and also from that of *B. massyae* in the great length of the cusps. The rhachidian is particularly long and narrow. The ovary was full of numerous large circular eggs measuring about 3 mm. in diameter.

*Remarks.*—See above p. 326. From *B. massyae* it differs in radula, web and funnel-organ. It differs from *B. ijimai* in external shape, in the fact that the funnel is more or less free and in the shape of the funnel-organ.

(?) **Bolitaena massyae** (Robson).

*Eledonella massyae*, Robson (1924, p. 202).
,, ,, ,, (1924*a*, p. 672, Pl. II, fig. 8, text-figs. 43–45).

*Type.*—In Brit. Mus. (Holotype.)
*Specimen seen.*—The type.
*Distribution.*—Off Cape Town, in 1014 fms.
*Description.*—The visceral sac is uniformly oval and its maximum width is 70% of its length. The head is very narrow (39%), the narrowest in fact of any of the described species. The arms are in the order 3.2.1.4, and there is not much difference between the length of the third arms and the rest. The third arms are short (43%). The first carry nine widely-placed suckers, the terminal 2–3 mm. being devoid of suckers. The second pair has 9–10 similar suckers and a similar bare apical area. The third pair has 10 suckers, of which the last three are very close together and decrease very rapidly. The fourth pair has been mutilated and only six suckers are visible. None of the suckers are abruptly enlarged. They are globular and devoid of any external constriction. The web is not very well preserved, but I think its formula is A = B = C.D.E. The deepest sector is about 28% of the arms, *i.e.* shorter than stated in the original description, and sector E is absent (?). The skin is quite smooth. The ground-colour is pale yellow and is covered with numerous rich purplish-brown chromatophores which tend to fuse together on the head and arms. The mantle-aperture is as usual widely open, but it is less wide than in *diaphana*. The funnel is rather broad and long and reaches about half-way towards the edge of the web. The funnel-organ is V-shaped with narrowly leaf-shaped limbs and a rounded apex. The median septum is well developed. The gills have 6–7 filaments in each demibranch. The radula has a rhachidian with three cusps a side which display a serial repetition as in the Octopodinae (cf. Part I, p. 12). The first laterals have five cusps, the second five or six, and there is a serial tendency for the first cusp to be double at every fourth tooth. On the whole, the radula tends to resemble that of *I. diaphana*, but the rhachidian is intermediate between those of *diaphana* and *E. pygmaea*.

The *nervous system*. The optic nerve is long and the peduncular ganglion is close to, but not in contact with, the optic ganglion. The optic ganglion is bilobed as in *E. pygmaea*.

The single available specimen is a female. The oviducts are stout, the sperm-oviducal glands small and the vaginae shorter than the oviducts and not so wide. I could find no trace of the aquiferous ducts.

*Remarks.*—This species is distinguished from *pygmaea* by (*a*) the narrowness of its head, (*b*) the size of the arms and (*c*) the radula. It differs from *E. ijimae* by (*a*) the narrowness of the head, (*b*) depth of the web, (*c*) form of the funnel-organ and (*d*) general shape.

**Bolitaena massyae,** subsp. **purpurea,** Robson.

*Eledonella massyae*, subsp. *purpurea*, Robson (1930*b*, p. 379, text-fig. 6).

*Type.*—In Brit. Mus. [Coll. R.S.S. " Discovery "]. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Only known from the type-locality, " Discovery " Stn. 86 (1926), 33° 25′ S., 6° 31′ E. in 547–0 fms. Taken in $4\frac{1}{2}$ m. townet.

*Description.*—The subspecies differs from the form which I described in 1924 in the following particulars. (1) The suckers are more widely spaced (6·5 mm. apart instead of 4·5 mm.). (2) The arms are a little shorter (54% instead of 56%). (3) The funnel-organ has thicker limbs. (4) The radula has two cusps a side on the median and four on the first lateral. The mesocone of the rhachidian is longer in the type. (5) The gills are much smaller, being 9% of the mantle length, instead of 16% as in the type. (6) The colour is deeper, and on the head the chromatophores tend to fuse together and to produce a very dark purple tint. In *C. diaphana* Joubin (1924, p. 43) found that " les viscères et le cerveau sont enfermés dans une vaste poche pleine de sang, qui envoie dorsalement deux grands prolongements cylindriques descendant jusqu'au fond du sac palléal . . . se rejoignent presque sur la ligne dorsale." In the present subspecies I found what I described as " a spacious cavity in which the viscera . . . are suspended." The cavity in the two forms seems to be identical.

*Remarks.*—I believe that this form is most closely related to *E. massyae*. The radula and funnel-organ are certainly distinctive; but it does not seem to differ from *massyae* in the bulk of its features.

### (?) **Bolitaena ijimai** (Sasaki).

*Eledonella ijimai*, Sasaki (1929, p. 13, Pl. VII, figs. 10–15).

*Type.*—In Tokyo Imperial University. (Holotype.)

*Distribution.*—Misaki, Sagami Province (Japan). Depth of catch not given. Found together with *Branchiocerianthus imperator*. Only known from the type-locality.

*Description.*—The animal is soft, " choroidal " and semi-transparent. The mantle is elongate, narrow, its width being just over half the length. The maximum width is across the eyes. There is a longitudinal keel-like ridge down the mid-ventral line as in *Iapetella prismatica* (Hoyle, 1886, p. 109), and the body seems to be laterally compressed (? accidentally). The eyes are rather small, though prominent, and are situated dorso-laterally. The arms are unequal. The third pair is as long as the body and " decidedly longer than the remaining pairs," which are about equal in length. There are about 15 suckers on each arm. They are separated until the middle of the arms, after which they become more closely set. The largest suckers, which are the 5th to 6th, are situated at the middle of the arm. The web is well developed and attains a maximum depth of about 50% of the arms. Its formula may be A = B.C = D.E. It " is quite rudimentary " in E.

The colour (in formalin) is a light drab. Sparse reddish-brown chromatophores are found, though they are closely crowded on both surfaces of web and arms. The visceral sac is covered with large blackish chromatophores.

The pallial aperture is wide. The funnel is entirely covered over by the tissues of the head. Its aperture is transversely elongated. The

funnel-organ is Λ-shaped and its limbs are short and thick. There is no funnel-valve.

The gill is very small and consists of 5 filaments aside. Sasaki does not mention any reduction of the inner demibranch (p. 326). The optic nerve is 2–3 times as long as the width of the brain. The peduncular ganglion is close to, but not in contact with the optic ganglion. No other details of the anatomy are given; but Sasaki supplies a clear figure of the central nervous system.

*Remarks.*—This species is distinguished from *pygmaea* by (1) its general shape, (2) the depth of the web, and (3) its large and prominent head. From *massyae* it is distinguished by the characters cited on p. 328.

**Eledonella,** Verrill (1884).

Elledonellids with a long optic nerve and the optic and peduncular ganglia remote. The third right arm (? hectocotylus) bears in the male a few very large suckers. Other characters as in the family.

*Type of the genus.—E. pygmaea,* Verrill.

For the status of this genus see p. 326.

**Eledonella pygmaea,** Verrill.

*Eledonella pygmaea,* Verrill (1884, p. 145, Pl. XXXII, fig. 2).
,, ,, Chun (1914, p. 20).
,, ,, Thiele (1915, p. 490, Pls. LXXXI, LXXXV, LXXXVI, text-figs. 54–56).
,, ,, Robson (1926*a*, *passim*).

*Type.*—In U.S. Nat. Mus. (? Holotype.)

*Distribution.*—37° 12′ N., 69° 39′ W., in 2949 fms. (Verrill; "Albatross" Stn. 2099); 28° 42′ N., 20° 0′ W., in 1641 fms.; 34° 5′ N., 33° 1′ W., in 1422 fms.; 36° 52′ N., 39° 55′ W., in 1641 fms. (Chun) ("M. Sars," Stns. 45, 53, 62); 1° 14′ N., 2° 10′ W., in 1914 fms. (Thiele) ("Valdivia," Stn. 53).

*Description.*—The following description is based on that of the type. The body is oblong-ovate, bluntly rounded apically. The maximum width is about 70% of the length ("length of body to edge of mantle above") and the width of the head is less (55%). The head is rather small and the eyes are of moderate size and not very prominent. The arms are distinctly short, the maximum length being 34%. The third arm is twice as long as the first and fourth. The web seems to be about 33% of the arm in sector B. Its shape is uncertain. From Verrill's data it seems that A is unknown, B and C are probably of equal depth (33%), D is much shallower and E is absent. The third right arm is said to be "hectocotylized" (cf. p. 15). It is shorter and stouter than its fellow. Beyond its middle point it bears four large urn-shaped suckers, the first of which is the largest. The basal part of these suckers is actually wider than the arm. The basal suckers on this and the other arms are of more moderate size and somewhat more widely spaced. There are 10–12 on each arm "besides a few minute ones at the tip." On the basal half of 3R there are 4 simple suckers. The colour is a pale bluish white spotted with large purple-brown chromatophores which are "arranged somewhat in rows on the outer surfaces of the arms." (For anatomy see p. 331.)

*Remarks.*—I feel very uncertain as to whether Thiele's figures, etc., ought to be applied to Verrill's species. One of Thiele's specimens was taken in the Guinea Stream and one ("M. Sars") from much farther north. The former (Pl. LXXXI, fig. 5) agrees fairly well with Verrill's description, but (*a*) the suckers are far more numerous, (*b*) the web is present between the fourth arms, (*c*) it is well developed in D, and (*d*) the arms are much longer. This specimen is unfortunately a female and does not show the characteristic enlarged suckers. The "M. Sars" specimens include males. In one a sucker on 3R is enormously enlarged and is over twice as large as the sucker next to it. The web seems less highly differentiated than in the type and the arms are much longer. If Thiele's diagnosis is correct, we must include his description of the jaws, radula, funnel-organ and nervous system (which are given below) in the specific diagnosis. The *jaws* are remarkably soft. The lower mandible has a rather shapeless rostral lamella and a long, narrow gular lamella. The *radula* resembles that of *diaphana* (Thiele, text-fig. 60), but (*a*) the main cusp of the rhachidian is longer and there seem to be fewer lateral cusps on that tooth, (*b*) the main cusp of the second lateral is a little higher in *diaphana* and there are more cusps, and (*c*) the third lateral is shorter in *pygmaea* (?). The *funnel-organ* is represented by a V-shaped strip (2·5–3 mm. wide), the halves of which form a right angle.

*Nervous system.*—The optic nerve is long and bears a little more than half-way along it a well-developed peduncular ganglion. The optic ganglion is in two portions.

### **Iapetella,** Hoyle, 1885.

("*Bolitaena*, Steenstrup" Chun; *Chunella*, Sasaki; *Bolitaenella*, Grimpe).

Eledonellids with short optic nerve. The hectocotylized arm bears several moderately enlarged suckers.

*Type of the genus.*—*I. prismatica*, Hoyle.

See remarks on p. 326.

### **Iapetella prismatica,** Hoyle.

*Iapetella prismatica*, Hoyle (1885, p. 231).
,, ,, (1885*a*, p. 107, fig.).
,, ,, (1886, p. 109, Pl. IX, figs. 1, 2).
(?) *Iapetella prismatica*, Hoyle (1904, p. 23, Pl. 5, figs. 10, 12).

*Type.*—In Brit. Mus. (Holotype.)

*Specimens seen.*—The type.

*Distribution.*—"Challenger" Stn. 126, off Rio San Francisco, Brazil, in 770 fms.; (?) "Albatross" Stn. 3414, off Tehuantepec, in 2232 fms.

*Description.*—The body is longer than broad (width-index 66%) and somewhat quadrate. The head is nearly as wide as the body (60%) and scarcely demarcated from the latter. The eyes are fairly large and prominent. In the median ventral line the body is raised into a prominent ridge, which, coupled with some degree of flatness of the dorsum, gave the animal a prismatic shape. The arms are in the order 3.1 = 2 = 4 (?) and are about 51% of the total length. The suckers are fairly close to begin with. Their size and spacing increase gradually up to the

middle of the arm, from which point they become smaller and closer together. In the "Albatross" specimen (see below) the suckers on the third arm are enlarged "exactly as figured by Verrill . . . in the case of *Eledonella pygmaea*." The suckers of the latter are very much larger than those figured by Hoyle. The web is of the form A.(?)B = C = D.E, and is about 26% of the longest arms (calculated). The body is gelatinous and semitransparent. Its surface is smooth, of a pale yellowish-grey ground-colour covered with numerous reddish-brown chromatophores.

The funnel is rather broad and barely reaches beyond the eyes. The funnel-organ in the type and "Albatross" specimen is Λ-shaped with broad, closely approximated limbs.

The gill has five filaments in the outer demibranch.

*Remarks.*—Hoyle did not describe his Mexican specimen, so I am unable to compare the two specimens.

This species is distinguished from *diaphana* by (1) its subquadrate body, (2) large head, and (3) shallow web, and from *heathii* by (1) its longer arms, (2) narrower and thicker funnel-organ, and (3) shallower web.

### **Iapetella diaphana** (Hoyle).

(Text-figs. 76–78.)

*Iapetella diaphana*, Hoyle (1885, p. 232).
,, ,, ,, (1885*a*, p. 108).
*Eledonella* ,, ,, (1886, p. 107, Pl. IX, figs. 3–6).
,, ,, Joubin (1900, p. 37, Pl. II, figs. 5–7).
,, ,, ,, (1903, p. 101).
,, ,, Hoyle (1904, p. 22, Pl. V, fig 11).
*Bolitaena* ,, Chun (1911 (?), p. 21).
,, ,, ,, (1914, p. 20, text-fig. 6).
,, ,, Thiele–Chun (1915, p. 493, Pls. LXXXII–LXXXIX, text-figs. 60–63).
*Eledonella diaphana*, Massy (1916*a*, p. 213).
*Bolitaena* ,, Joubin (1918*a*, p. 40).
*Eledonella* ,, ,, (1920, p. 33).
,, ,, ,, (1920*a*, p. 1).
*Chunella* ,, Sasaki (1920, p. 171).
*Bolitaena* ,, Thiele (1920, p. 434) (juv.).
,, (*Eledonella*) *diaphana*, Joubin (1924, p. 42, Pls. III, VII, XII, XIII).
*Chunella diaphana*, Sasaki (1929, p. 14, Pl. VIII, figs. 1–4).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—0° 42′ S., 147° E. (N. of New Guinea), in 1100 fms. (Hoyle, '86); E. Tropical Pacific (E. of Galapagos Is., S.E. of Acapulcõ, off Acapulcõ, Kwajalong Id. (Marshall Archipelago)), in 664–1897 fms. (Hoyle, '04); 27° 27′ N., 14° 52′ W., in 1423 fms.; 34° 51′ N., 33° 1′ W., in 875–1422 fms.; 36° 53′ N.; 29° 47′ W., in 164 fms. (Chun); 12 hauls, Sierra Leone, Equatorial Atlantic, Indian Ocean (Seychelles–Sumatra, etc.), in 2188–601 fms. (Thiele); Laccadive Sea and Andaman Is., 870–705 fms. (Massy); between Madeira and Morocco, in 2385 fms. (Joubin, 1900); off Cape Verde Is., in 1355 fms.; Azores, in 0–1094 fms.; 36°

54′ N., 11° 49′ W., in 0–2789 fms.; 36° 05′ N., 9° 0′ W., in 0–2002 fms. (Joubin, 1920); Gorringe Bank, in 0–2352 and 2188 fms.; N.W. of Madeira (Stns. 3128, 3131), in 0–1914 fms.; off Madeira, in 0–1641, –1094 and 547 fms. (Joubin, 1924); equatorial Atlantic and S. of the Azores, in 1641, –1094–727 fms. (Thiele, 1920); off Kii Province, Japan, in 720 fms. (Sasaki, 1920).

Fig. 77.—*Iapetella diaphana*. Funnel-organ.
(*a*) After Thiele (1915); (*b*) after Sasaki (1929); (*c*) after Hoyle (1904).

*Description.*—It is uncertain whether all the forms placed in this species were correctly determined. For the time being I have treated them as conspecific, but the status of various forms is discussed below.

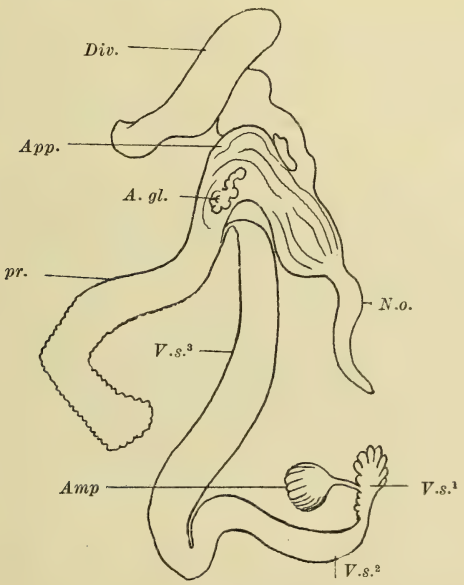



Fig. 78.—*Iapetella diaphana*. Reproductive system (♂). (After Chun, 1915.)
*A. gl.*, acinose gland; *app.*, appendix; *amp.*, ampulla; *N.o.*, Needham's organ; *pr.*, prostate; *Div.*, penial diverticle; *V.s.*, seminal vesicle.

The animal is apparently rather small, though Thiele does not give the magnification, if any, of the large specimen on his Plate LXXXII. The mantle is oblong-ovate, 74–56% of the length, and the head is narrower (55–30%). The head is short and in the type the eyes are large and rather prominent. The arms are in the order 3.2 = 4.1 (etc.). In the

type they are 50 of the total length and range from 33% to 50% (from Thiele's Plate 81, fig. 5, they may be calculated as 58–60%). The number, shape and size of the suckers is very uncertain. They seem on the whole to be rather small and closely placed, sometimes in contact and crowded so as to become triangular in section. In Joubin's (1900) specimen they are quite separate. Thiele (*l.c.*, Pl. LXXXII, fig. 4) figures one with abrupt enlargement at the fourth, the size of the enlarged suckers very gradually diminishing outwards. The web has the form B = C = D.A.E in the type. Its shape is uncertain in the rest. Joubin (1900) says it is absent in E. The depth-index is 75 (Joubin, *l.c.*, text) – ? 28 (type). The external surface is quite smooth, its ground-colour pale with numerous (? rather elongate) reddish-brown (Chun–Thiele, figs.) chromatophores. The funnel is fairly prominent and reaches two-thirds of the distance towards the web-edge in the type, less (one-third) in Thiele's large specimen. The greatest discrepancy in the descriptions is in the funnel-organ which is ⩓-shaped in Sasaki's specimen, ⩔-shaped in Hoyle's E. Pacific form and △-shaped in Thiele's (cf. fig. 78). There is no valve (cf. Hoyle (1886 and *l.c.*)) and no adhesive-organ. There are 6–7 filaments in each demibranch. The inner demibranch, as in *B. massyae*, is only half as deep as the outer and the area of the gill is very small. The median

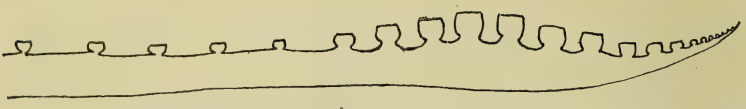


Fig. 79.—Diagram of position of suckers on arm of *Vitreledonella alberti*. (Mus. Océanogr., Monaco.)

adductor is well developed. The radula has a rhachidian with a very wide base and low mesocone. In Thiele's figure this is shown as about half as long as the base is wide. There are three ectocones on each side. The first lateral has four cusps subequal in height, of which the inner is somewhat stouter. The second lateral is plainly variable. The third lateral is of moderate stoutness and marginal plates are present. The details of the alimentary tract (Chun, Sasaki), nervous system (Joubin, Chun) and vascular, excretory and reproductive system (Chun) are known in some detail. The posterior salivary glands are larger than the anterior. The crop is enormous. The stomach and crop are remarkably small in comparison with the liver. There seems to be a set of specialized pancreatic cells (Chun) imbedded in the surface of the liver. Sasaki (*l.c.*) makes the very interesting statement that in his specimen the ink-sac is free of the liver. The ink-sac is apparently small (Chun, Sasaki). The male organs are very interesting and seem on the whole to be specialized. The proximal vas deferens bears a large ampulla, and there is an accessory gland on the prostate. Needham's organ is relatively very small and narrow, and the vas deferens widens out very considerably just where it enters the penis. The latter bears a stout diverticle.

*Remarks.*—I am afraid it is useless to attempt to decide the status of the various forms included in this species. The lack of comparable data for all the specimens and the defective descriptions of some make it quite impossible to say if they are conspecific or not. The differences

in the funnel-organs of Hoyle's E. Pacific, Thiele's and Sasaki's specimens are very marked. The depth of the web in Joubin's specimen of 1900 (from text) as compared with that of the type, the similar differences between the size of the arms in the type on the one hand and in the specimens of Joubin and Sasaki on the other, as well as the crowded or widely spaced suckers (*q.v.*), are all suggestive of subspecific, or even specific differences.

**Iapetella heathi** (Berry).

*Eledonella heathi*, Berry (1911, p. 589).
„ „ *id.* (1912*a*, p. 276, Pl. XXXII, fig. 4; Pl. XXXIII, figs. 2–4).

*Type.*—In U.S. Nat. Mus. (Holotype.)

*Distribution.*—Only known from the type-locality, off Santa Catalina Island, California, in 2228 fms. (" Albatross," Stn. 4396).

*Description.*—The mantle is ovoid and its width is 74% of its length. The head is short, broad (58% of the mantle-length) and well defined. The eyes are large and prominent. The arms are in the order 3.2.4 = 1 and 41% of the total length, *i.e.* rather short even for a member of this group. The suckers are urceolate and, as in Chun's figure of *diaphana*, increase in size abruptly at the third and then slowly diminish from that point outwards. The web at its deepest is about 33% of the arms. It is subequal, but C. and D. are deeper than A, B, and E. The tissues are " subgelatinous to membranous." The colour (in alcohol) is " nearly white with a few sparsely scattered brown chromatophores; on the heap and outer surfaces of the arms these are very minute and more or less longitudinal in arrangement."

The mantle-aperture is very wide. The funnel is short and does not extend beyond the eyes. The funnel-organ is Λ-shaped with rather narrow limbs, which are pointed at the base. The gills are " large and prominent " and consist of 8–9 lamellae ( ? in each demibranch).

*Remarks.*—As the specimens placed in *diaphana* are different in so many details (*v. supra*), it is very hard to decide if Berry's species is clearly distinguished from it or not. It differs from typical *diaphana* in (*a*) its less prominent funnel; (*b*) more numerous gill lamellae; and (*c*) the less disparity between the third and fourth arms. The latter are not so disproportionate in Thiele and Sasaki's specimens. The funnel-organ of Berry's species agrees fairly well with that of Sasaki's, but the extremities of the limbs in the former are more acute. The species differs from *prismatica* by the characters cited on p. 332.

Family 2. Amphitretidae, Hoyle, 1886.

The pallial aperture is reduced to two small orifices on each side. The eyes are " telescopic," dorsal in position and closely approximated. The hectocotylized arm has a distal flattened part equipped with suckers transformed into knobs and a proximal triangular-grooved expansion. The radula is like that of the Bolitaenidae. The funnel-organ and penis are like those of *Octopus*.

**Amphitretus,** Hoyle, 1885.

With the characters of the family.

*Type of the genus.—A. pelagicus*, Hoyle.

The anatomy of this interesting genus is as yet incompletely known. Until the central nervous system and alimentary canal are fully described, it is impossible to discuss its affinities properly. So far we may say that the radula and gill are very like those of *Bolitaena*, and I do not think that the highly specialized and peculiar type of radula would have been acquired independently. On the other hand, the funnel-organ and penis are very like those of the Heteroglossa. The almost complete closure of the mantle-cavity and the form of the hectocotylus are peculiar, though an approximation to the latter is seen in *Vitreledonella translucida* (Robson, 1930*b*, p. 381). For the time being the genus is best retained in the Ctenoglossa.

Although there is a marked tendency in the Order for the mantle-aperture to be reduced in width, its reduction in this genus as the result of a median-ventral and lateral fusion of the mantle-edge to the head, is quite isolated and appears quite discontinuously. Similar closure occurs in the Decapoda (p. 57, see also p. 219). Nothing as yet is known of the habits of *Amphitretus*.

**Amphitretus pelagicus,** Hoyle.

*Amphitretus pelagicus*, Hoyle (1885, p. 235).
,, ,, ,, (1885*a*, p. 113, fig.).
,, ,, ,, (1885*b*, p. 271, fig. 106).
,, ,, ,, (1886 (p. 67, Pl. IX, figs. 7–9).
,, ,, Ijima and Ikeda (1902, p. 85, Pl. II, text-figs. 1–3).
,, ,, Chun (1903*a*, p. 88).
,, ,, Berry (1912, p. 397 (name only)).
,, ,, Thiele (1915, p. 532, Pl. XCI, figs. 6–10, text-figs. 64–66).
,, ,, Sasaki (1917, p. 361, figs. 1–2).
,, ,, Robson (1925, p. 107).
,, ,, ,, (1926*a passim*).
,, ,, Sasaki (1929, p. 16, Pl. III, figs. 1–2; Pl. VIII, fig. 5).

*Type.*—In Brit. Mus. (Holotype.)

*Specimen seen.*—The holotype.

*Distribution.*—Off the Kermadec Is., in 520 fms. (Hoyle); Okinose, Sagami Sea, in 312 fms. (long-line) (Ijima and Ikeda); Tateyama Bay, Sagami Sea, on shore after storm (Sasaki); 34° 31′ S., 26° 0′ E., Agulhas Stream, in 984 fms. (Thiele).

*Description.*—During life " a thick layer of a delicate, colourless and perfectly transparent gelatinous tissue " covers the whole of the animal. In preservatives the outer coat tends to contract and become discoloured and wrinkled. The head is not demarcated from the body, but the eyes in Hoyle's and Thiele's description are very prominent and may be described as telescopic. Sasaki (*l.c.*, p. 16) says that the eyes in his specimen " do not protrude beyond " the surface; but it is not clear if this projection is beyond the main surface or beyond the choroid coat. The body is very wide according to Hoyle's figures (index = 122), less wide in the Japanese specimens ( ? 100–88) and relatively narrow (from the figure) in Thiele's specimen. The arms are short (66–62% of the total length).

The suckers are uniserial to begin with, but tend to be biserial beyond the edge of the web. They are under 8% of the mantle-length in the type. The web is very deep (over 80%) in the type and more or less equal. It is shallower in the Japanese examples (76–71, both from figures) and Thiele's (about 50), but seems more or less equal in these, except in Ijima and Ikeda's specimen in which A is far deeper than E. The funnel (type) was fairly prominent and extended about one-third of the way to the mantle-edge. Its degree of freedom from the head seems to depend on how much of the external gelatinous coating is left. There is no valve in the funnel and no trace of an adhesive system. The funnel-organ is W-shaped and its limbs are of equal length. The mantle-aperture is reduced to two lateral orifices (see p. 336). There are ten filaments in each demibranch in the type, Ijima and Ikeda's and Sasaki's specimens. The ink-sac is present and the anal valves are well developed. The jaws are soft and flat. The radula is known only from Thiele's specimen. The median tooth has a large mesocone and three small ectocones on each side. The admedian is 4-cusped, the largest cusp being second from the inside. The third tooth is 5–6 (?)-cusped, the largest cusp being as in the preceding tooth. The fourth tooth is a narrow blade like that of *Octopus*, and there is a marginal plate. In one of Sasaki's specimens the third right arm is hectocotylized. Its tip is slender and gradually tapering for about 14 mm., and the flattened inner surface shows a series of minute paired knobs (? modified suckers). Proximally there is found a swelling, the surface of which is Λ-shaped, the apex pointing distally. The oral surface of this swelling is traversed by a groove. The proximal edge of the groove bears a small prominence. The arm is furnished with a well-developed copulatory groove. The penis is like that of *Octopus* (Sasaki, 1917), and has a large globular diverticle. The oviducts and vaginae are of moderate length, and there is a circular oviducal gland.

*Remarks.*—I have already pointed out (1930*b*, p. 384 and foll.) that it is not at all certain that the type and the other described forms are conspecific. Sasaki's description fits that of the type fairly well, except that the animal seems narrower, the suckers are smaller and the eyes are less prominent. The same is true of Ijima and Ikeda's examples. On the other hand, Thiele's specimen seems to have a much shallower web.

### **Amphitretus thielei,** Robson.

*Amphitretus thielei*, Robson (1930*b*, p. 383, Pl. III, fig. 2, text-figs. 11–13).

? " *Amphitretus pelagicus*, Hoyle," Thiele (1915, p. 532).

*Type.*—In Brit. Mus. [Coll. R.S.S. " Discovery "]. (Holotype.)

*Specimen seen.*—The type.

*Distribution.*—Only known from the type-locality, 33° 50′–34° 13′ S., 16° 04′–15° 49′ E., " Discovery " Stn. 101, in 0–218 fms.

*Description.*—The single specimen so far described has been distorted, and it would appear to have had the gelatinous coat found in *pelagicus* either removed or closely shrunk to the body. The outer tissues are more or less transparent, and are traversed by a network of thick fibres. The body is elongate-ovoid and the head very narrow. The eyes are dorsal

in position and actually in contact in the middle line, a feature not noted in the other species, in which the eyes are merely described as "close together." The contact between the eyes in *thielei* is closer than that figured by Thiele. The arms were probably subequal and about 67% of the total length. The suckers are uniserial and widely spaced to begin with, though distally they seem to have been alternating. At about the thirteenth they become much larger. They are simple in structure and very thick-walled. The web is about 50% of the arms, and its sectors were probably subequal. The funnel is largely adherent to the head and extends about one-third of the way from the eyes to the edge of the web. The funnel-organ is large and broadly W-shaped. There is no trace of a valve. There are 7–8 filaments in each demibranch. The inner demibranch is very much reduced, as in *Bolitaena*, being only half as deep as the outer. The mandibles are very weak and imperfectly chitinized. They are not so much splayed-out as in Thiele's figure of *pelagicus*, and differ in many details especially in the disposition of the pigmented thickenings of the inferior mandible. The radula differs from that of *pelagicus* as figured by Thiele (text-fig. 66). The first and second laterals have more cusps and the main cusp is larger and the other cusps are smaller. The vaginae are very thick and large and remind us of those of *Bolitaena massyae* (Robson, 1924*a*, text-fig. 44). As in *B. massyae* the spermoviducal gland is small.

*Remarks.*—It has already been shown that Thiele's specimen of "*pelagicus*" may not be rightly named. As *thielei* was taken west of Cape Town, not very far from the spot where Thiele's specimen was obtained (though the stations are separated by the Agulhas "divide"), it may be thought that they must be conspecific. Thiele's "*pelagicus*" was, however, only very imperfectly described. The size of the arms and web is alike in the two. The radula and mandibles are very unlike, the eyes of *thielei* are less prominent and more closely adherent than in Thiele's form. I do not think they should be treated as conspecific. The "Discovery" species seems to be unlike the Kermadec-Japanese specimens of *pelagicus*, *e.g.* in the depth of the web, number of gill-filaments and width of mantle (see Robson, *l.c.*, table, p. 385). Sasaki alludes to the pallial orifices in *pelagicus* being small and leading "into a compressed passage." In *thielei* the orifices are nearly 20 mm. long, and the only suggestion of a passage is that on the head side there is a downward-hanging flap of skin, the "lateral infundibular fold" of Ijima and Ikeda (*l.c.*, p. 92 and fig.).

### Incertae Sedis.

### **Heptapus,** Joubin, 1929.

*Definition.*—There are only seven arms, which are represented by a single median dorsal one and three symmetrically disposed pairs (lateral and ventral). There is a deep web about 75% of the arms in length. The suckers are mainly alternating. There is no adhesive-organ. The funnel is buried in the tissues of the head, and its apex is represented by a round hole. The pallial septum (? comprising the median adductor) is present. The tissues are gelatinous and semi-transparent. The velar

area is bent towards the dorsal surface, as in *Retroteuthis*, but the web is not adherent to the tissues of the dorsum.

*Type of the genus.*—*H. danai*, Joubin.

*Remarks.*—This genus was proposed by Joubin for an enigmatic specimen, having seven arms and no trace of either a normal or a hectocotylized eighth arm. The rest of the description does not allow one to form any opinion of its family position. It is not a Cirromorph, and the lack of adhesive apparatus, the gelatinous tissues and deep web suggest that it is a form of *Alloposus*, perhaps near *A. hardyi*. In the latter there is the same rotation of the velar area, but in *A. hardyi*, as in *Retroteuthis*, the latter is adherent to the dorsum.

Examples of Octopods with seven arms, though very rare, are not unknown. The British Museum has recently acquired, through the kindness of Mr. C. Oldham, a specimen of *Eledone cirrosa* in this condition, and Lönnberg (1899, p. 51) states that a specimen of *Octopus patagonicus* showed this condition.

**Heptapus danai,** Joubin.

*Heptapus Danai*, Joubin (1929*a*, p. 11, text-figs. 14, 15).

*Type.*—In the Carlsberg Institute, Copenhagen. (Holotype.)

*Distribution.*—Off Cape Hatteras, in 54 fms. ("Dana" Stn., 1349. III).

*Description.*—The body appears to be widely oval and saccular. The surface "opposite the arms" (? that away from which the arms are reflected) is described as "bombée, presque hémisphérique." The eyes are very large. There are only seven arms. The longest is median, unpaired and dorsal, the remaining six being disposed in three symmetrical opposed pairs, which decrease in length towards the ventral aspect. The suckers are disposed at first uniserially, then in two widely alternating rows. The largest are those at the point where the alternation starts. The suckers are arranged as follows :—

1st arm : 6 uniserial suckers of moderate size followed by 4 large pairs, 2 moderately large pairs, 6 small pairs and 10 microscopic pairs.

2nd arms : 5 uniserial suckers of moderate size followed by 3 large pairs, 3 moderate, 3 small and 10 microscopic pairs.

3rd arms : 5 uniserial suckers of moderate size followed by 3 large, 3 moderate and 6–7 microscopic pairs.

4th arms : 4 uniserial suckers of moderate size followed by 3 large, 3 moderately large, 2 small and 5 microscopic pairs.

The suckers are prominent and thick-rimmed.

The velar area lies inclined towards the dorsal surface at an angle of 90° to the main axis of the body, but the web is not fused with the dorsal integument.

The web is thick and very deep, being 75% of the arms in length. The funnel is buried in the tissues in the head and its extremity does not project, but is seen as a round hole in the skin.

The pallial aperture seems to be wide, but this is by no means certain. There is no adhesive apparatus. The pallial septum is thick and solid,

but it is not clear whether any part of it is constituted by the median adductor.

The mandibles are present and are surrounded by a single lip. The tissues are gelatinous and soft. There is a large number of brown and yellow chromatophores in the skin.

*Remarks.*—It is possible, as Joubin says, that this is an abnormal specimen. He makes no suggestion as to the family to which it would belong, and his description does not allow me to venture more than the suggestion put forward on p. 339.

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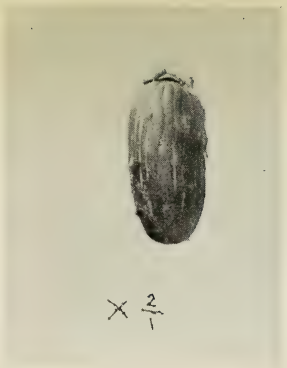
PLATE I.

1




2

3

4

Fig. 1.—Egg of *Grimpoteuthis meangensis* × 2. Fig. 2.—Eggs of unknown Octopod from a deep-sea cable (A, p. 166). Fig. 3.—Eggs of unknown Octopod from a deep-sea cable (B, p. 166). Fig. 4.—*Grimpoteuthis* sp. A (Brit. Mus.).

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FIG. 1.—*Grimpoteuthis umbellata*. "Michael Sars," Stn. 53.

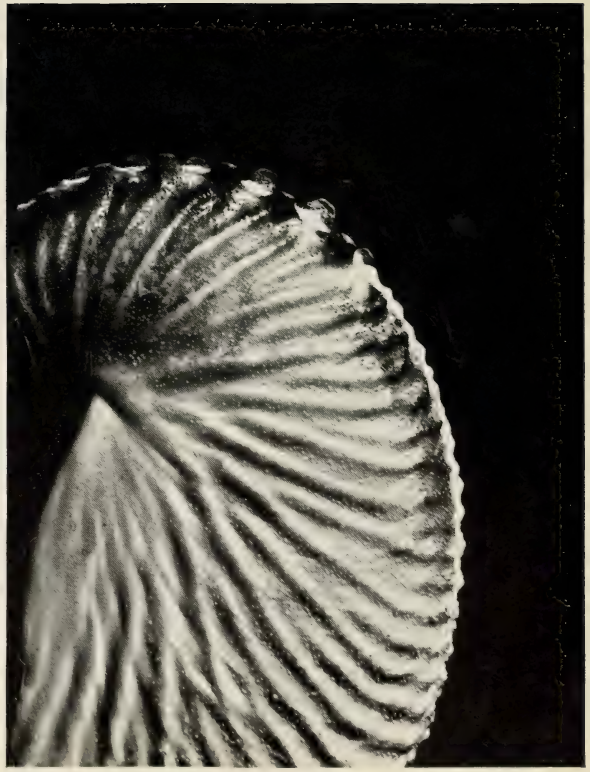

FIG. 2.—*Argonauta nouryi* × 4 (showing surface sculpture).

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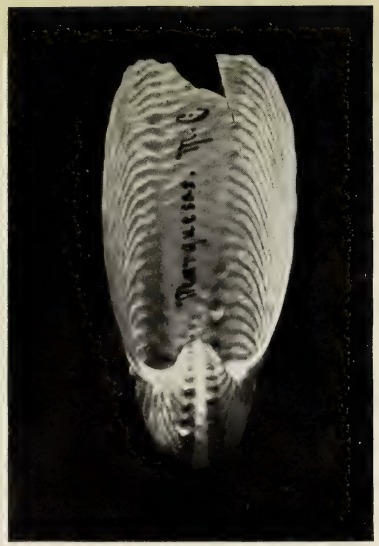

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FIG. 1.—*Argonauta nouryi*. FIG. 2.—*Teretoctopus indicus* (type). FIG. 3.—*Teretoctopus alcocki* (type).

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Fig. 1.—*Benthoctopus profundorum* (type).

Fig. 2.—*Grimpella thaumastocheir* (type).

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PLATE V.

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FIG. 1.—*Parcledone polymorpha*, form *affinis* (type). FIG. 2.—*Parcledone* sp. FIG. 3.—*Thaumeledone brevis* (type).

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PLATE VI.

Fig. 1.—*Bathypolypus arcticus* (type). Fig. 2.—*Bathypolypus arcticus* (square-bodied form).

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